Manual of Nearctic Diptera

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Volume 2

Coordinated by

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CONTENTS

	Preface	J. F. McAlpine	v
49	Lonchopteridae	B. V. Peterson	675
50	Platypezidae	Edward L. Kessel	681
51	Phoridae	B. V. Peterson	689
52	Syrphidae	J. R. Vockeroth and F. C. Thompson	713
53	Pipunculidae	D. E. Hardy	745
54	Conopidae	Kenneth G. V. Smith and B. V. Peterson	749
55	Cypselosomatidae	J. F. McAlpine	757
56	Micropezidae	George C. Steyskal	761
57	Neriidae	George C. Steyskal	769
58	Tanypezidae	George C. Steyskal	773
59	Strongylophthalmyiidae	George C. Steyskal	777
60	Psilidae	George C. Steyskal	781
61	Diopsidae	B. V. Peterson	785
62	Lonchaeidae	J. F. McAlpine	791
63	Otitidae	George C. Steyskal	799
64	Platystomatidae	George C. Steyskal	809
65	Pyrgotidae	George C. Steyskal	813
66	Tephritidae	Richard H. Foote and George C. Steyskal	817
67	Richardiidae	George C. Steyskal	833
68	Pallopteridae	J. F. McAlpine	839
69	Piophilidae	J. F. McAlpine	845
70	Clusiidae	Á. Soós	853
71	Acartophthalmidae	J. F. McAlpine	859
72	Odiniidae	J. F. McAlpine	863
73	Agromyzidae	K. A. Spencer	869
74	Opomyzidae	J. R. Vockeroth	881
75	Anthomyzidae	J. R. Vockeroth	887
76	Aulacigastridae	H. J. Teskey	891
77	Periscelididae	J. F. McAlpine	895
78	Asteiidae	Curtis W. Sabrosky	899
79	Milichiidae	Curtis W. Sabrosky	903
80	Carnidae	Curtis W. Sabrosky	909
81	Braulidae	B. V. Peterson	913
82	Coelopidae	J. R. Vockeroth	919
83	Dryomyzidae	George C. Steyskal	923
84	Sciomyzidae	Lloyd V. Knutson	927
85	Ropalomeridae	George C. Steyskal	941

86	Sepsidae	George C. Steyskal	945
87	Lauxaniidae	G. E. Shewell	951
88	Chamaemyiidae	J. F. McAlpine	965
89	Heleomyzidae	Gordon D. Gill and B. V. Peterson	973
90	Trixoscelididae	H. J. Teskey	981
91	Chryomyidae	J. F. McAlpine	985
92	Rhinotoridae	J. F. McAlpine	989
93	Sphaeroceridae	S. A. Marshall and O. W. Richards	993
94	Curtonotidae	J. F. McAlpine	1007
95	Drosophilidae	M. R. Wheeler	1011
96	Diastatidae	J. F. McAlpine	1019
97	Camillidae	J. F. McAlpine	1023
98	Ephydridae	Willis W. Wirth, Wayne N. Mathis, and J. R. Vockeroth	1027
99	Chloropidae	Curtis W. Sabrosky	1049
100	Cryptochetidae	J. F. McAlpine	1069
101	Tethinidae	J. R. Vockeroth	1073
102	Canacidae	Willis W. Wirth	1079
103	Scathophagidae	J. R. Vockeroth	1085
104	Anthomyiidae	H. C. Huckett	1099
105	Muscidae	H. C. Huckett and J. R. Vockeroth	1115
106	Calliphoridae	G. E. Shewell	1133
107	Oestridae	D. M. Wood	1147
108	Sarcophagidae	G. E. Shewell	1159
109	Rhinophoridae	D. M. Wood	1187
110	Tachinidae	D. M. Wood	1193
111	Hippoboscidae	T. C. Maa and B. V. Peterson	1271
112	Nycteribiidae	B. V. Peterson and Rupert L. Wenzel	1283
113	Streblidae	Rupert L. Wenzel and B. V. Peterson	1293
	Corrections and addenda to Volume 1		1303
	Index		1307

PREFACE

J. F. McALPINE

The main purpose of the *Manual of Nearctic Diptera* is to provide a modern, well-illustrated, easily interpretable means for identifying the families and genera of two-winged flies of America north of Mexico. Volume 1, which contains Chapters 1–48, provides the general background for this work and includes individual treatments of all the families of the suborder Nematocera and the lower Brachycera of the Nearctic Region.

Volume 2 continues the work begun in Volume 1 by providing similar individual treatments of the families of the infraorder Muscomorpha (Cyclorrhapha, higher Diptera). In all, it contains 64 chapters, numbered 49–113. Chapters 49–53 treat the five families of the section Aschiza, and Chapters 54–113 treat the 60 families of the section Schizophora. Volume 2 also contains a subject index, as well as a list of the corrections and addenda for Volume 1.

The numbering sequence for the family chapters in Volume 2 follows that proposed in the table of classification on pages 2 and 3 in Volume 1. Similarly, the terminology and the patterns of treatment employed in Volume 1 are maintained in Volume 2.

Some changes from what is stated in Volume 1, relating to the contents, organization, and authorship of certain parts of Volume 2, have occurred since Volume 1 was published.

Mr. J. A. Downes, now retired, decided against completing a general treatment of the habits and environments of Diptera, and regretably, that chapter was canceled.

Additional authors have become associated with some chapters in Volume 2, as follows (newly associated authors are italicized):

- Chapter 54. Conopidae, by Kenneth G. V. Smith and *B. V. Peterson*
- Chapter 89. Heleomyzidae, by Gordon D. Gill and *B. V. Peterson*
- Chapter 93. Sphaeroceridae, by *S. A. Marshall* and O.W. Richards
- Chapter 98. Ephydridae, by Willis W. Wirth, Wayne N. Mathis, and *J. R. Vockeroth*
- Chapter 105. Muscidae, by H. C. Huckett and *J. R. Vockeroth*

Also, the treatment of the evolution of the Diptera, which was originally planned to appear as a single chapter under joint authorship in Volume 2, is excluded here. It will appear later as Volume 3 of the Manual comprising three independently prepared chapters, as follows:

- Chapter 114. Phylogeny and classification of the Nematocera, by D. M. Wood and A. Borkent
- Chapter 115. Phylogeny and classification of the orthorrhaphous Brachycera, by N. D. Woodley
- Chapter 116. Phylogeny and classification of the Muscomorpha, by J. F. McAlpine

Aside from enabling us to complete the work on schedule and to present it in more practical-sized volumes, this tactic allows for healthy differences in analytical approaches, in assessment and interpretation of facts, and in the presentation of results. It also has the merit of bringing the expertise of two fresh minds to bear on this difficult subject.

We wish to acknowledge again all the authors listed under this heading in Volume 1. Without them the Manual could not have been produced. It is with sadness and a deep sense of loss that we note the death, on 3 December 1981, of one of our most highly respected contributors, Dr. C. P. Alexander (Byers 1982). The following new author, whose contribution appears in Chapter 93, Volume 2 (Sphaeroceridae, with O. W. Richards), is additional to those listed on pages i-iii in Volume 1:

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A general acknowledgment is made here to all those who provided special assistance throughout the production of the Manual. Many people have kindly reviewed certain chapters, or parts thereof, and many others have sent us important material for study and illustration. Bruce Cooper, especially, provided highly valued assistance to many authors by personally testing keys for clarity and accuracy. We are also appreciative of those who informed us about errors and omissions detected in Volume 1 and offered suggestions for improvement. These items are incorporated in the "Corrections and Addenda to Volume 1," published at the end of Volume 2. Finally, we wish to reiterate our appreciation to the late G. P. Holland, W. B. Mountain, and D. F. Hardwick, past directors of the Centre, and especially to G. A. Mulligan, our present director, for encouragement and managerial support instrumental in completing this project.

As in Volume 1, the illustrations greatly enhance the usefulness and appearance of Volume 2, and for these we again pay a very special tribute to our main artist, Ralph Idema. He is an outstanding contributor to both volumes. In all, Volume 2 contains 1912 illustrations assembled on 287 plates. Most of these are original drawings completed by Mr. Idema, but the 62 figures on nine plates for the families Tephritidae, Platystomatidae, and Pyrgotidae were prepared by Barry Flahey. Much credit is also due to Bruce Cooper for labeling all the illustrations for Volume 2, and we are again indebted to B. Edwards and R. St. John, Cartography Section, Land Resource Research Centre, for their fine cooperation in carrying out the photomechanical work needed for producing the final plates.

Special recognition and thanks are extended to Sharon Rudnitski, Research Program Service, for the literary and technical editing services she provided in both volumes. Her expert help in processing all of the text for style, consistency, and accuracy of typography, spelling, and cross references; in verifying all bibliographic and figure references; and in overseeing all aspects of publication is greatly appreciated.

The excellent cooperation received from Marie Labelle and members of the stenographic staff of the Biosystematics Research Centre, especially Diane Beauchamp, Eileen Muir-Fashola, and Rosanna Menchini, for typing and retyping the many revisions of the various chapters is gratefully acknowledged.

Reference

Byers, G. W. 1982. In Memoriam, Charles P. Alexander 1889–1981. J. Kans. ent. Soc. 55: 409–417.

LONCHOPTERIDAE

49

B. V. PETERSON

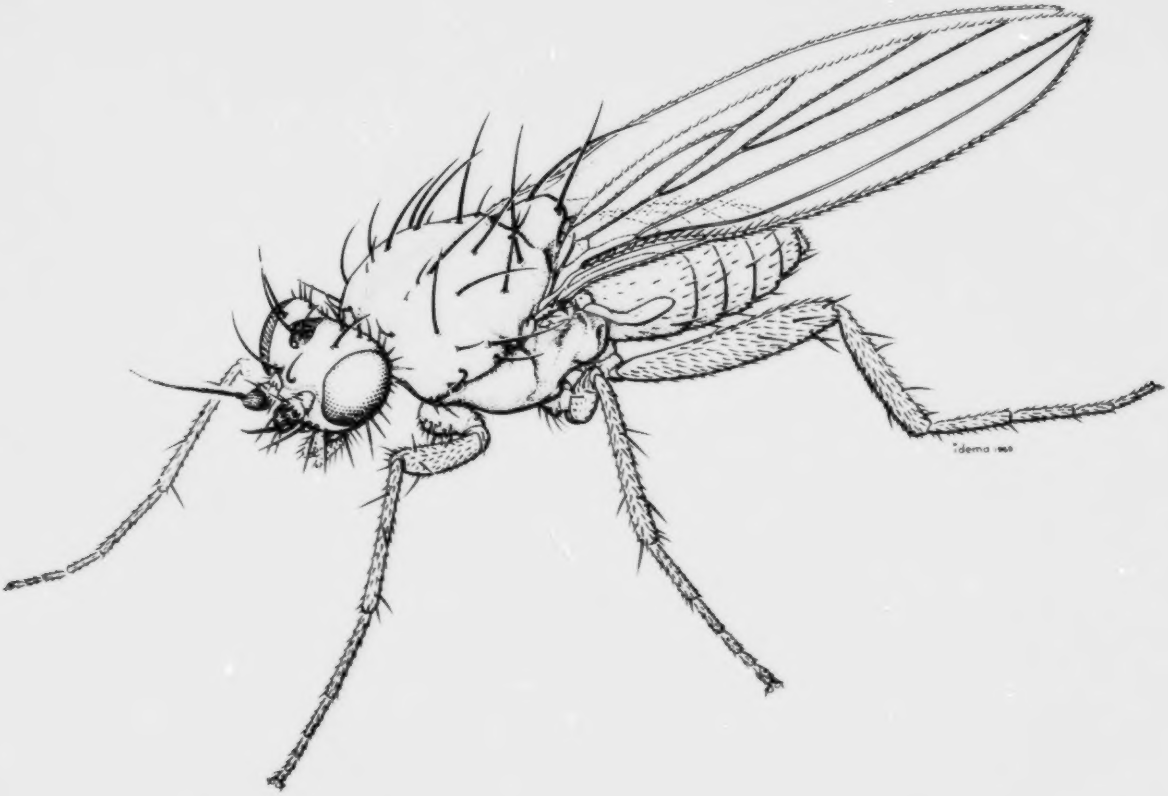


Fig. 49.1. Female of *Lonchoptera furcata* Fallén.

Small slender yellowish to brown flies (Fig. 1), ranging in length from about 2.0 to 3.8 mm. Head as wide as or wider than thorax; eyes broadly separated in both sexes. Wing rather long, slender, and somewhat pointed, with characteristic venation that shows sexual dimorphism; in male $A_1 + CuA_2$ terminating in hind margin of wing (Fig. 3); in female $A_1 + CuA_2$ joining CuA_1 and terminating in wing margin as $A_1 + CuA_2 + CuA_1$ (Fig. 2).

Adult. Head: as wide as and usually slightly wider than thorax, more than twice as wide as long, slightly concave posteriorly (Fig. 1). Frons short and broad, bare except for a pair of strong divergent lower interfrontal bristles medially above antennae. Chaetotaxy: a pair of upper orbital bristles, a pair of ocellar bristles, a pair of convergent inner vertical bristles, and a pair of short convergent postocellar bristles present; true outer vertical bristles absent; a row of postocular bristles extending ventrally and slightly anteriorly onto postgena; dorsalmost bristle of this series on each side considered by most authors to be an outer vertical bristle, but this pair of bristles is convergent whereas true outer vertical bristles are divergent; a series of occipital bristles extending ventrally onto postgena also present on each side of occiput; vibrissae strong; four or five subvibrissae on lower margin of gena. Face short, slightly depressed medially; frontogenal suture weak but usually evident. Antennae short, with bases widely separated; all segments small; scape and pedicel each with a row of short bristles on distal margin; pedicel bowl-like; first flagellomere largest of all segments, hemispherical; pedicel and first flagellomere fitting together somewhat like two halves of a ball; arista subapical, short pubescent, with three aristomeres; apical aristomere often as long as or longer than head. Eye only moderately large but prominent, obliquely higher than long, bare, with a variably small triangular or crescent-shaped emargination on inner margin; ocelli small, all subequal in size and nearly equidistant from each other, and all situated on a small variably raised tubercle. Proboscis short; palpus short, clavate, with short setae only.

Thorax: subrectangular, longer than high, convex dorsally (Fig. 1). Antepronotum narrow, ring-like; postpronotum small, not strongly differentiated, in some cases weakly differentiated; proepisternum with a series of about two to four short bristles above fore coxa; precoxal bridge complete although sometimes tenuously so. Anterior spiracle small. Scutum rather strongly arched anteriorly, less convex posteriorly; presutural and postsutural areas of scutum variously but not strongly delineated. Scutellum moderately large, subtriangular in shape, rounded posteriorly, flattened dorsally. Postnotum only moderately large, of nearly uniform length across its surface; laterotergite slightly convex but conspicuous. Pleural sclerites of thorax weakly differentiated. Chaetotaxy: a single bristle on postpronotum; one presutural and two postsutural supra-alar bristles, one presutural and one postsutural intra-alar bristle, and two posterior notopleural bristles present; in addition three presutural and three postsutural dorsocentral bristles also usually present, with anterior two bristles of this series, especially second bristle, and prescutellar dorsocentral bristle reduced and stoutly hair-like; two apical bristles on scutellum; pleural region of thorax bare. Posterior spiracle small.

Legs moderately long and slender; claws and pulvilli small; empodia apparently absent. Fore coxa long; anterior surface setose, with one or more long and several short anterior bristles; posterior surface generally bare but usually with one posterodorsal and several posteroventral setae. Hind femur slightly swollen; femora and tibiae variously bristled, with number and distribution of these bristles taxonomically important; fore tarsus of male slightly swollen.

Wing (Figs. 2, 3) usually distinctly longer than entire body, slender, broadest near middle and tapering distally, with a narrow rounded to acutely pointed apex; anal lobe and alula not developed; most veins setulose dorsally; membrane generally yellowish brown. C complete, continuing around wing although weakened behind R_{4+5}, without costal breaks; Sc complete, bare; R_1 short, ending in C just behind Sc, with dorsal setae; R_{2+3} and R_{4+5} arising from a short petiole, and long and straight or slightly curved, with their apices convergent; R_{2+3} bare dorsally; R_{4+5} setose dorsally; crossvein r-m relatively long, nearly horizontal; M_1 and M_2 rather straight, reaching wing margin; stem of M between crossvein r-m and fork of M_1 and M_2 apparently lost, replaced by crossvein dm-cu; M_2, CuA_1, and sometimes M_1 setose dorsally along their entire length; CuA_2 separate for a short distance basally; A_1 running close to hind margin of wing near base; CuA_2 and A_1 fused over most of their length, setose dorsally, and reaching wing margin in male (Fig. 3); in female $CuA_2 + A_1$ joining with CuA_1 well before margin of wing and reaching it as $A_1 + CuA_2 + CuA_1$ (Fig. 2). Calypteres small. Halter moderately large; stem usually shorter than elongate knob.

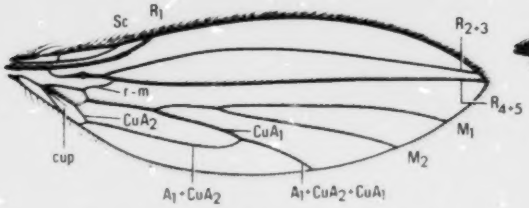
Abdomen: relatively short, subcylindrical to oval. Tergites and sternites of both sexes beset with a sparse but varying array of long and short setae; sternite 1 varyingly discernible, sometimes distinct but hidden between hind coxae and a much larger sternite 2. Seven spiracles present in both sexes, sometimes in membrane (Fig. 4), sometimes in margins of tergites (Fig. 6).

Female with tergites 1–8 (syntergite 1 + 2 plus tergites 3–7) appearing as six visible tergites when abdomen not extended; tergite 8 reduced and telescoped under tergite 7; tergite 9 membranous or represented by a faint narrow band closely associated with posterior margin of tergite 8, and sometimes weakly articulating with a similar ventral sternite. Stuckenberg (1963) thought tergite 8 to be small or absent, and considered tergite 9 to be present. Epiproct (probably with elements of tergite 10) small but usually distinct, sometimes clearly articulating with hypoproct (probably with elements of sternite 10); cercus small to moderately large, variously setose (Fig. 4). Sternite 9 varying from a weak somewhat Y-shaped structure to a tiny sclerotized bar to being barely discernible; hypoproct varying from small but distinct with minute setae to being barely discernible. Two spermathecae apparently present, unsclerotized and difficult to see, described by de Meijere (1906) as two ducts, each with a border of large cells at its apex forming a cylindrical envelope.

Male with tergites 1–7 (syntergite 1 + 2, tergites 3–5, and syntergite 6 + 7) appearing as five visible tergites when abdomen not extended. Sternites 3 and 4 often with one or a few pairs of stout setae; sternites 6 and 7 usually membranous but when present, e.g. in *Lonchoptera uniseta* Curran, both sternites are separate and distinct; sternite 6 in *L. uniseta* represented by a weakly sclerotized band that has a more heavily sclerotized plate-like central portion and lateral margins which enclose spiracle 6 and unite with anteroventral margins of syntergite 6 + 7; sternite 7 in *L. uniseta* broader, densely sclerotized, with a double pad-like swelling medioventrally on each side that houses spiracle 7 and is characterized by a small brush-like patch of short setae. Tergites 6 and 7 fused (Fig. 6) (Hennig (1976) suggested tergites 7 and 8 were fused); syntergosternite 8 distinct but variably developed, usually represented by a heavily sclerotized narrow strap-like sclerite closely associated with the structures of the genital complex, a possible remnant of a portion of sternite 8 present in *L. uniseta* (Fig. 6). Epandrium well-developed but varying in size from small to nearly as long as segments 4 and 5 combined, folded anteriorly under these segments. Cercus moderately large

Figs. 49.2–7. Wings, abdomens, terminalia, and larva: wing of (2) *Lonchoptera furcata* Fallén and (3) *L. uniseta* Curran; (4) abdomen of *L. furcata*, ventral view; (5) terminalia of *L. uniseta*, left lateral view; (6) abdomen of *L. uniseta*, ventrolateral view; (7) larva of *Lonchoptera* sp., dorsal view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; gonex apod, gonocoxal apodeme; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spm pmp, sperm pump; spr, spiracle; st, sternite; syntg, syntergite; syntgst, syntergosternite; tg, tergite.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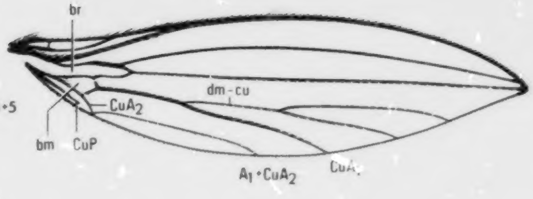
2 Lonchoptera furcata ♀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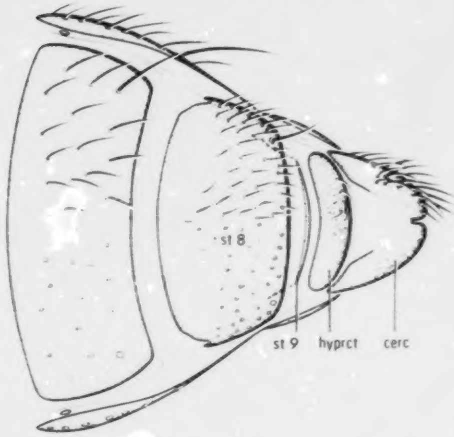
3 Lonchoptera uniseta ♂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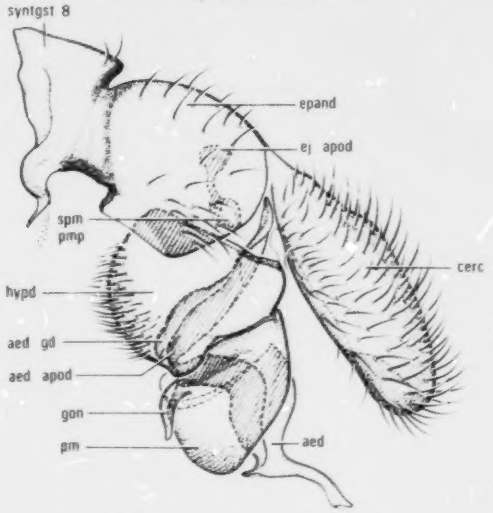
4 Lonchoptera furcata ♀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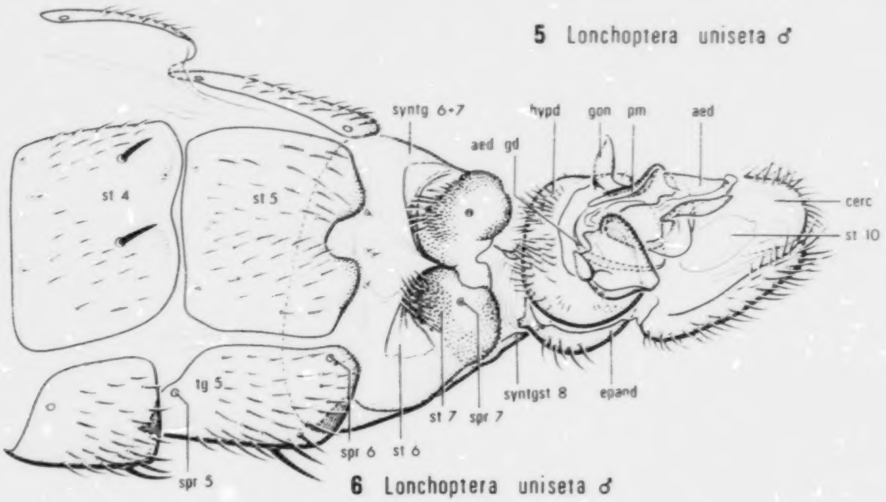
5 Lonchoptera uniseta ♂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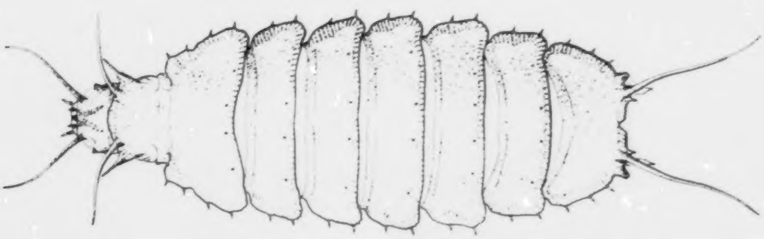
spr 6
st 6
spr 5

6 Lonchoptera uniseta ♂



7 Lonchoptera sp.

to large in relation to epandrium (Fig. 5), variously setose, and sometimes with a ventral accessory lobe or spines, or both. Surstyli absent. Hypandrium often heavily sclerotized, usually a narrow somewhat U-shaped sclerite, articulating with base of epandrium dorsally; hypandrium sometimes weakly developed and more or less fused with bases of gonopods. Gonopod composed of a single element varying in size and taking various forms, sometimes with accessory lobe or spines, or both; gonocoxal apodeme short, slender, rod-like. Paramere usually well-developed, varying considerably from rather simple and pad-like to highly complex in structure. Aedeagal apodeme short but well-developed, articulating ventrally with a median aedeagal guide of varying size and form; aedeagus of varying size and form, with broad and sclerotized basal section, sometimes tapering distally to a slender often recurved apex that may be varyingly bifurcate; sperm pump and ejaculatory apodeme present but usually small. Sternite 10 varying from membranous to a variously shaped heavily sclerotized plate, bearing various small to stout bristle-like setae, and sometimes with lateral processes.

Egg. Small, about 0.6 mm long and 0.25 mm in diameter, white when laid, oval to reniform in shape depending on angle of viewing. Chorion without pattern or specialized structures. First described and portrayed by de Meijere (1900, 1906).

Larva. Description based on a single larva (Fig. 7) available to the author. Somewhat fusiform in shape, narrower anteriorly, broader and more blunt posteriorly, convex dorsally, more flattened ventrally, 4.3 mm long. Respiratory system amphipneustic. Tracheal system described by Whitten (1956).

Head short, somewhat retractile. Antenna short, two-segmented; distal segment shorter and paler than basal segment. Mandibles and tentoropharyngeal skeleton sclerotized and somewhat darkened, extending to metathorax; maxillary palpus minute, consisting of a single segment; labium with somewhat swollen subconical labellum-like structures that project laterally beyond margin of head and have a series of canals or pseudotrachea-like structures ventrally as well as minute pale setae.

Prothorax partially sclerotized dorsally, membranous ventrally, somewhat retractile; anterodorsal margin with two long submedian bristle-like processes. Anterior spiracle situated on a short stalk near posterolateral margin of prothorax. Mesothorax membranous, allowing partial retraction of prothorax under metathorax. Metathorax membranous ventrally but with a sclerotized plate dorsally on anterior half; this dorsal plate bearing two long submedian bristle-like processes, and having a narrow but distinct, somewhat crenulate flange on its anterior margin that terminates on each side with one moderately long bristle-like process and one shorter and stouter spine-like process; disc of metathoracic plate with numerous crescentic ridges and rows of spots; metathorax, as described here, called mesothorax by some authors.

Abdominal tergites 1 and 2 fused into syntergite 1 + 2; a faint but discernible transverse fusion line evident near middle of this plate; syntergite 1 + 2 wrongly named metathorax plus abdominal segment 1 by Lundbeck (1916) and others; a row of four minute but distinct tubercle-like processes, two of which are submedian and two sublateral, evident on each half of this plate, as on tergal plates 3–8; presence and position of these tubercles on tergal plates 3–8 similar to those on first visible tergite, confirming that this plate is composed of fused tergal plates 1 and 2. A somewhat crenulate flange present on both lateral and posterior margins of tergal plates 1 (1 + 2) to 8 (seven visible tergites), broader on lateral margins, projecting wing-like over venter, and bearing one short anterolateral and one short posterolateral spine-like process; flange of tergal plate 8 with three short spine-like processes on each side. Tergal plate 8 largest, bearing two long sublateral bristle-like processes; base of each of these processes medially with a short posteriorly directed spine-like process. Posterior spiracles situated lateral to bases of these processes, each borne on a short stalk. Another featureless plate perhaps composed of two fused plates present posterior to tergal plate 8 and projecting ventrally from it. Ventral surface of abdomen with only vague evidence of segmentation, covered with numerous narrow transverse ridges of varying size. Pleural region of each abdominal segment with a minute conical spine-like projection; hind margin of terminal segment with six such processes.

The larva upon which the above description is based, from France, agrees well with the basic description and figures of *Lonchoptera lutea* Panzer by de Meijere (1900, 1906) and Smith (1969*a*). The larva (probably also *L. lutea*) was first described and illustrated by Lubbock (1862) from England. De Meijere (1900, 1906), Lundbeck (1916), Hennig (1952), and Smith (1969*a*) have described the larva of *L. lutea*, and Nielsen *et al.* (1954) presented figures of the larva of *L. furcata* (Fallén) from Iceland. They mentioned that *L. furcata* could be distinguished from *L. lutea* by the shape of the lateral processes, namely the margins of the abdominal tergal plates, which are long, slender, and pointed. Baud (1973) presented figures of the larvae of *L. tristis* Meigen and *L. fallax* de Meijere, in addition to those of *L. lutea* and *L. furcata*.

Puparium. Briefly described by Lundbeck (1916). Puparium resembling larva, but with small darkened protruding anterior spiracles. Adult emerging through a T-shaped split extending from thorax to anterior abdominal segments.

Biology and behavior. The biology and behavior of the Lonchopteridae remain generally unknown. Except for the work of Baud (1973), no detailed biological accounts have been published; only scattered notes in the literature are available.

Larvae and pupae have been found among dead leaves and decaying plant remains in gardens, forests, and meadows in both dry and moist locations. The food of the larva is unknown, but in the laboratory Stalker (1956) noted that larvae fed on microorganisms found in damp dead leaves but did not complete their development on this type of food. Adults are known to occur, often in large numbers, in humid places near streams or ponds, in shady woods with thick leaf carpets (Smith 1969*a*), in rocky tidal zones near the coast (Dahl 1960), in bogs and moist grassland near brooks, springs, and even hot springs (Nielsen *et al.* 1954), and in dry-meadow (Andersson 1970) and mountain-meadow vegetation (Stalker 1956). Stalker (1956) examined the contents of the crop and concluded that the adult must feed chiefly or entirely on nectar. He was able to maintain adults in good condition in the laboratory for as long as 7 months on a diet composed of water and honey. He also found that females caught when reproductively active would, at times, oviposit on almost any surface, wet or dry, in the laboratory. He suggested that *Lonchoptera furcata* (as *dubia* Curran) could produce two or three generations a year, and that females caught in the fall and maintained in the laboratory would oviposit the following spring. Adults have a characteristic jerky movement somewhat like that of the Phoridae. Most known species are bisexual. In some species, such as *L. furcata*, the male is apparently rare or nonexistant, and the female is parthenogenetic at least over part of its range. Collin (1938) suggested that the males of *L. furcata* were crepuscular and therefore were missed by those collecting earlier in the day. However, Andersson (1970) swept males from vegetation in full sunshine on the Vestman Island of Bjarnarey, Iceland. He suggested that males of *L. furcata* appear as an atavism from time to time and that small, isolated bisexual populations can redevelop under certain favorable ecological conditions. Vandel (1938), Stalker (1956), Guénin and Stocker (1961), and Baud (1970, 1973) have studied various aspects of parthenogenesis in the family. Lonchopterids are reported to be heavily parasitized by various hymenopterous species of the families Ichneumonidae, Braconidae, and Pteromalidae (Lundbeck 1916, Smith 1969*a*).

Classification and distribution. The Lonchopteridae is a small, widely distributed, and easily recognized family. Rapp and Snow (1945) cataloged 23 world species. Today, about 35 species have been described, all of which are placed in the genus *Lonchoptera* Meigen. At one time, *Cadrema lonchopteroides* Walker was tentatively placed in this family but it is now included in the Chloropidae. Four species of *Lonchoptera* are currently recognized in the Nearctic region, namely *borealis* Curran, *occidentalis* Curran, *uniseta* Curran, and the cosmopolitan *furcata* (Fallén). Saigusa (1975) indicated there were about 30 undescribed species known from the Oriental region. With further collecting and study, perhaps other new Nearctic species may be recognized, as was suggested by Stalker (1956).

The name *Musidora* Meigen, 1800 has frequently been used as the valid generic name. However, the publication in which this name appeared was suppressed by the International Commission on Zoological Nomenclature in 1963. Now, *Lonchoptera* Meigen, 1803 is almost universally accepted as the correct generic name.

De Meijere's 1906 revision of the Palaearctic species was the first major taxonomic study of the family. In this work de Meijere recognized the usefulness of the characters of the male terminalia in separating species. Duda (1927) improved on his work by recognizing the value of the chaetotaxy of the legs for species discrimination. Czerny (1934) updated the knowledge on the Palaearctic species and provided keys to the various color forms of *L. lutea* and *L. furcata*. These color forms are generally ignored in modern literature. Hennig (1976) provided a useful discussion on the male terminalia and phylogeny of the family. Some other useful extralimital taxonomic studies on the family include those of Lundbeck (1916), Collin (1938), Andersson (1966, 1970, 1971), Smith (1969*a*, 1969*b*), and Stuckenberg (1963). Descriptions and a key to the four Nearctic species are given by Curran (1934).

The relationships of this anomalous family remain somewhat obscure. The family has been placed in both the orthorrhaphous and the cyclorrhaphous Brachycera by various authors. Most authors have regarded the family as being somewhat remote from the other Brachycera. For example, Griffiths (1972) placed the Lonchopteridae as the only family in his subphalanx Acroptera (of the phalanx Cyclorrhapha), and the rest of the Cyclorrhapha in the subphalanx Atriata. On the other hand, Hennig (1976) refuted the arguments of those who considered the Lonchopteridae as the sister group of the other Cyclorrhapha. This family probably is best placed as a highly specialized member of the Platypezoidea rather than in a superfamily by itself. More work is necessary to establish fully the relationships of the Lonchopteridae to the other families of Diptera.

Rohdendorf (1974) stated that, "Paleontological records consist only of the remnants of some species of the genus *Musidora* in the abundant fauna of Baltic amber; Mesozoic fossils are unknown." However, Bachofen-Echt (1949) mentioned that Musidoridae (Lonchopteridae) were not known in Baltic amber, and Hennig (1973) makes no mention of any known fossil Lonchopteridae.

The only genus in the family, *Lonchoptera*, is represented by the four Nearctic species listed above.

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PLATYPEZIDAE

50

EDWARD L. KESSEL

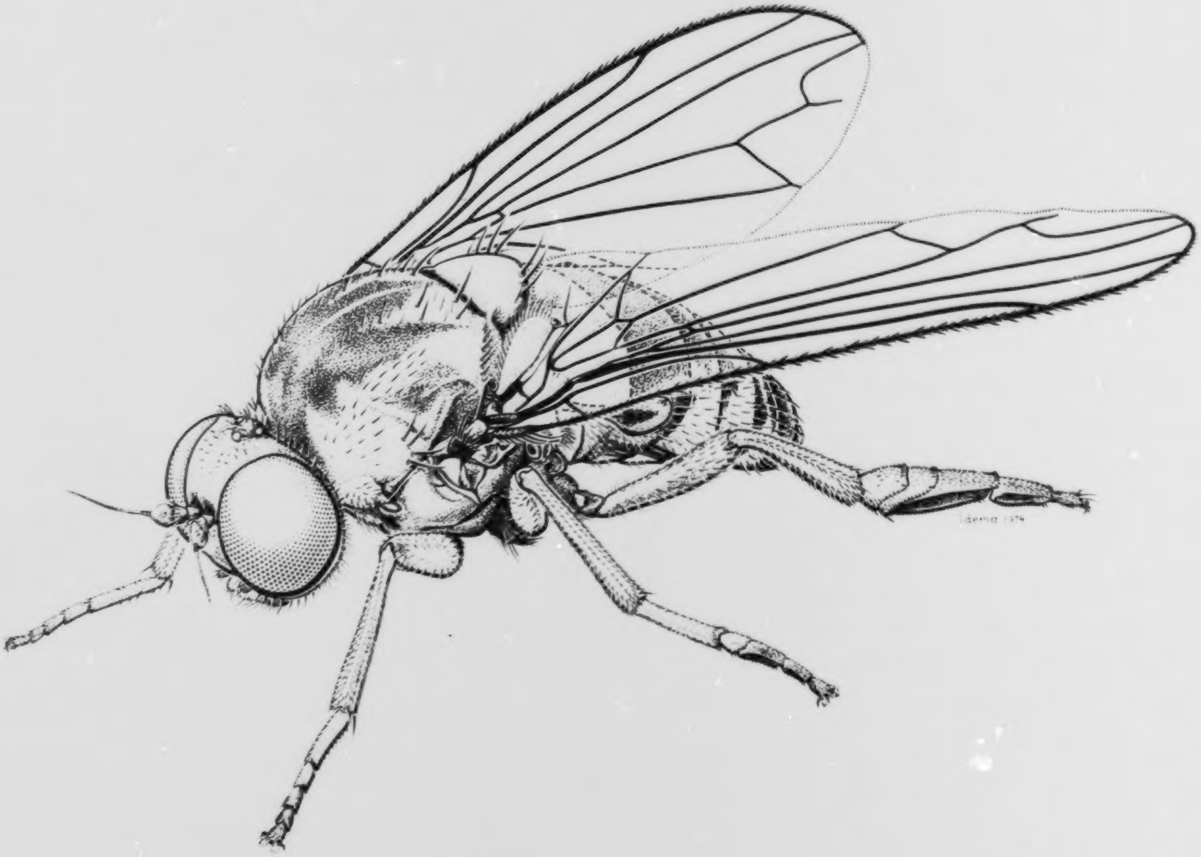


Fig. 50.1. Adult female of *Plesioclythia agarici* (Willard).

Slender or plump flies, 2–10 mm long (Fig. 1); color black, gray, yellow, orange, or brown, or combinations of these, sometimes marked with shining blue or green. Wing clear or brownish, always with a relatively large cell cu*p*. Hind tarsus usually flattened.

Adult. Head: as broad as thorax, rounded in front, flattened behind. Mouthparts short and fleshy. Antenna with bare terminal arista; scape and pedicel short and subequal; scape sometimes with a single prominent dorsal bristle; pedicel with a distal whorl of bristles; first flagellomere variable in length and outline, typically covered with short fine hair. Male holoptic, with compound eyes meeting for a distance of 8–20 ommatidia; eye red, divided into an upper area of larger ommatidia and a lower region of smaller ones; female dichoptic, with all ommatidia small. Ocellar tubercle prominent, especially in male, with two to five pairs of ocellar bristles; anterior pair (greater ocellar bristles) frequently much longer than others, located just in front of posterior ocelli; bristles of frontal area absent or displaced in male; only female with obvious orbital and frontal bristles; vertical bristles absent in male, but outer ones present in female of some genera; postocular bristles well-developed.

Thorax: transverse suture indicated only at sides (Fig. 20). Acrostichal bristles in a single median row in Opetiinae and Platypezininae (Fig. 20) but undifferentiated or lacking in Platypezinae; dorsocentral bristles usually arranged in two uniserial rows of well-developed bristles with posteriormost few becoming progressively larger (Fig. 20), but in *Polyporivora* Kessel & Maggioncalda, all tiny and multiserial; usually with two weak postpronotal bristles present; presutural intra-alar bristles often lacking or not differentiated from lateroclinate presutural dorsocentral bristles; presutural supra-alar bristle usually present, often accompanied by one or more setulae; notopleural bristles always present and strong, variable in number, usually arranged in two rows; postsutural intra-alar bristles small, arranged in one short to long row; postsutural supra-alar bristles present in some genera, e.g. *Callomyia* Meigen and *Agathomyia* Verrall (Fig. 20), but lacking in *Bertamyia* Kessel and *Platypezina* Wahlgren; postalar bristle strong, often accompanied by one or more setulae; postsutural intra-alar bristle very strong; scutellum usually with two, but sometimes with up to four pairs of marginal bristles. Wing (Figs. 2–19) clear or uniformly brown; pterostigma darkened in some forms (Fig. 3); C unbroken, extending to M_1; cell C asymmetric (shaped like scalpel blade) (Figs. 2–12, 18) or symmetric (shaped like spearhead) (Figs. 13, 16, 17); crossvein r-m usually present, absent in *Microsania* Zetterstedt (Fig. 3); R_1 usually bare but microscopically setulose in *Callomyia* (Fig. 4); R_{2+3} and R_{4+5} unbranched; crossvein dm-cu present (Fig. 8) except in Opetiinae (Figs. 2, 3); M_{1+2} branched (Figs. 8–15) or unbranched (Figs. 2, 4–7); cell cu*p* always well-developed and ending in an acute angle.

Legs of Platypezinae stout; posterior tarsus expanded in width and bilaterally flattened in both sexes but more obviously so in female, except in *Calotarsa* Townsend where male has posterior tarsus widened and ornamented (Fig. 24); soles well-developed on third and fourth tarsomeres of hindleg of female in Platypezinae. Legs of Opetiinae and Platypezininae moderately slender in female, but posterior tibia and posterior tarsus of male more or less cylindrically expanded; proximal tarsomeres of hindleg of male sometimes greatly dilated as in *Microsania*, *Platypezina*, and *Grossoseta* Kessel & Kirby; dilated segments not flat in life, but often in dried specimens becoming collapsed, flattened, and even curled; fore femur in male of *Agathomyia*, *Bertamyia*, *Callomyia*, and *Grossoseta* with strong curved spine (safety-pin bristle) near base (Fig. 22).

Abdomen: elongate, especially in Platypezininae, and cylindrical or somewhat flattened, often with long slender hairs at sides in male (Fig. 21). Circumversion of terminalia occurring in two stages, the first 180° taking place in pupa and remaining 180° within a few minutes after emergence from puparium; male terminalia (Figs. 21, 2.132, 2.133) complex and variable; female terminalia (Fig. 23) simple, telescopically retractile, with three sclerotized spermathecae.

Larva. Typically with a head and 11 body segments (Figs. 25–33), usually flattened, but sometimes cylindrical. Head poorly differentiated, fairly unsclerotized, and indistinctly set off from first body segment; short tubercle-like antenna located above rudimentary palpus (Fig. 28). Body of most forms with marginal processes laterally, typically with one pair per segment, except for segments 2 and 11, which have more; usually smaller dorsal processes also present on segments 3–10; segments 3–10 often bearing bristles, but bristles always lacking on segments 1, 2, and 11. Spiracles located at ends of wrinkled tube-like spiracular processes; anterior pair on segment 1; posterior ones (Fig. 26) on segment 11.

Puparium. Similar to larva in detail, except dorsal processes frequently more conspicuous in puparium. For a detailed treatment of the immature stages, see Kessel et al. (1973).

Biology and behavior. Adults, either on the wing or running about erratically on leaves of bushes in filtered sunshine, are observed most frequently in damp woods. They are sometimes found individually hovering in deep shade or in swarms of dancing males in forest openings. The females are attracted to these swarms, where aerial coupling takes place; immediately after coupling, the paired flies settle with heads in opposite directions on low bushes until mating is completed. For the many platypezids that frequent filtered-sunshine areas, feeding begins at midmorning after most birds have retired to digest breakfast. The flies feed actively, moving to-and-fro over the leaves and stopping often to ingest honeydew or other food. Then suddenly, later in the morning when the sun reaches a specific angle peculiar to each species, all platypezid activity ceases. This period of inactivity corresponds to the time of day when the birds next prefer to feed. Midday is therefore a poor time to collect. The flies reappear in the afternoon when the sun sinks to the angle that initiated the rest in the morning and continue feeding until the sun settles to the angle that signaled the morning feeding period. Again, platypezid activity is timed to cease before most birds begin looking for their evening meal.

Adults of *Microsania* are attracted to smoke or the odor of smoke. They are best collected by sweeping through smoke over fires, but they can also be attracted by using the aerosol-dispensed smoke-odor vapor used by apiculturists. *Microsania* larvae are unknown; they are presumed to feed on fungi, like the larvae of other members of the family.

The eggs of platypezids are laid between the gills or in the pores of the fungi on which the larvae feed. When the host is a soft fungus, oviposition is limited to the one day after the spores have developed during which the fungus is still firm and fresh. Females are easily collected while they are ovipositing and often remain undisturbed while the fungus is picked, carried indoors, and placed upside down. The larvae develop quickly, especially in short-lived soft fungi. In the long-lasting leathery or woody kinds, larval growth can be interrupted repeatedly by periods of diapause, which allow survival of the larvae whenever the host plant dries out. Larval growth is resumed as soon as the tissues are refreshed by moisture. Pupation takes place in the soil or litter of the forest floor, or in cocoons formed in the litter. Emergence of adults from puparia can occur within a few days following pupation, but it is sometimes delayed by pupal diapause for many months. Some species have several generations a year, and others have one. Peak emergence is in the autumn at most latitudes, but in Alaska and the Yukon and at high altitudes, peak emergence begins in June.

Adults of some species have been reared from larvae found in fungus hosts and, presumably, the larvae of all platypezids feed on fungi, although hosts of only a few species are known. Some fungi are known to serve as hosts for flies of various genera, and some species of fly can utilize a variety of fungi.

Classification and distribution. The family consists of three subfamilies, with 23 genera and about 215 described species. All the subfamilies, 18 of the genera, and 71 of the species occur in North America. The five genera not represented in North America are *Opetia* Meigen with four species from Europe and Japan, *Lindneromyia* Kessel and *Pamelamyia* Kessel from Africa, *Orthovena* Kessel & Buegler from Europe, and the controversial *Atelestus* Walker (=*Platycnema* Zetterstedt) (Kessel 1960) of Europe, which some would place in the Empididae.

Nine North American genera have been proposed since the family was described in the previously published catalog of North American Diptera (Kessel 1965): *Bertamyia* Kessel; *Grossoseta* Kessel & Kirby; *Seri* Kessel & Kessel; *Symmetricella* Kessel; and *Grossovena*, *Paraplatypeza*, *Penesymmetria*, *Plesioclythia*, and *Polyporivora*, all by Kessel and Maggioncalda.

Keys to genera

Adult

1. Crossvein dm-cu absent (Figs. 2, 3) .... OPETIINAE....2
Crossvein dm-cu present (Figs. 4–19) 3

2. Crossvein r-m present; M_{1+2} not branched (Fig. 2) .... ***Melanderomyia*** Kessel
1 sp., *kahli* Kessel; Kansas to Pennsylvania; Kessel 1960
Crossvein r-m absent; M_{1+2} branched, but with anterior branch incomplete at base (Fig. 3) .... ***Microsania*** Zetterstedt
2 spp.; widespread; Kessel 1947

3. Acrostichal bristles present, in a distinct uniserial median row (Fig. 20) .... PLATYPEZININAE....4
Acrostichal bristles absent, but occasionally with a few small scattered setulae in this position .... PLATYPEZINAE....8

4. M_{1+2} branched (Figs. 8, 9) 5
M_{1+2} not branched (Figs. 4–7) 6

5. Furcation of M_{1+2} well beyond crossvein dm-cu (Fig. 8). Fore femur of male with a strong black anteroventral bristle near base (Fig. 22). Cell cu*p* usually longer than apical section of A_1 in both sexes (Fig. 8) .... ***Grossoseta*** Kessel & Kirby
1 sp., *pacifica* (Kessel); Pacific Coast, California to British Columbia; Kessel and Kirby 1968
Furcation of M_{1+2} proximal to, exactly at, or barely beyond crossvein dm-cu (Fig. 9). Fore femur of male without strong anteroventral bristle near base. Cell cu*p* usually shorter than apical section of A_1, at least in female (Fig. 9) .... ***Platypezina*** Wahlgren
2 spp.; eastern, New Hampshire to Michigan; Kessel 1948, 1961*a*

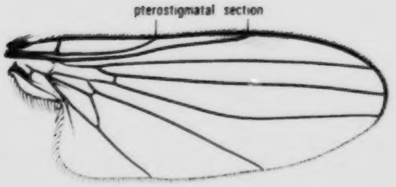
6. R_1 setulose (Fig. 4) .... ***Callomyia*** Meigen
10 spp.; widespread; Kessel and Buegler 1972
R_1 without setulae 7

7. Plane of crossvein r-m crossing at apex of cell c (Fig. 5). Postsutural supra-alar bristle absent. Male terminalia without surstyli .... ***Bertamyia*** Kessel
1 sp., *notata* Loew; Oregon to Quebec, south to California and Virginia; Kessel 1970
Plane of crossvein r-m crossing near middle of cell c (Fig. 6). Postsutural supra-alar bristle present (Fig. 20). Male terminalia with surstyli .... ***Agathomyia*** Verrall
26 spp.; widespread; Johnson 1916, Kessel 1949 and 1961*b*

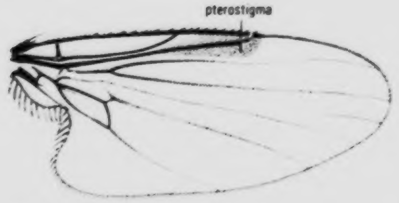
8. M_{1+2} not branched (Fig. 7) .... ***Metaclythia*** Kessel
1 sp., *currani* Kessel; Ontario to Wisconsin; Kessel 1951
M_{1+2} branched (Figs. 10–19) 9

9. Cell cu*p* over twice as long as apical section of A_1 (Fig. 10). Dorsocentral bristles in irregular rows .... ***Polyporivora*** Kessel & Maggioncalda
2 spp.; widespread; Kessel and Maggioncalda 1968
Cell cu*p* about equal in length to apical section of A_1 (Figs. 11–19). Dorsocentral bristles in regular rows 10

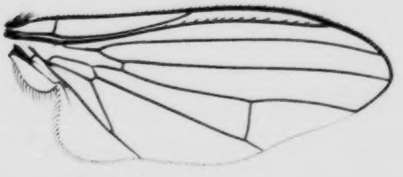
10. Furcation of M_{1+2} nearer to crossvein dm-cu than to wing margin (Fig. 11) .... ***Seri*** Kessel & Kessel
1 sp., *dymka* (Kessel); Pacific Coast, California to British Columbia; Kessel and Kessel 1966
Furcation of M_{1+2} usually nearer to wing margin than to crossvein dm-cu (Figs. 12–19)....11


pterostigmatal section

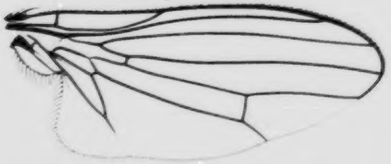
2 Melanderomyia sp. ♀


pterostigma

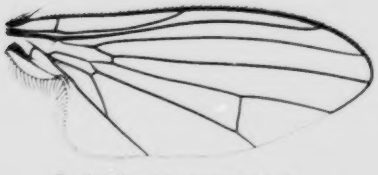
3 Microsania sp. ♂



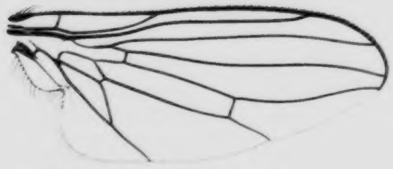
4 Callomyia calla ♂



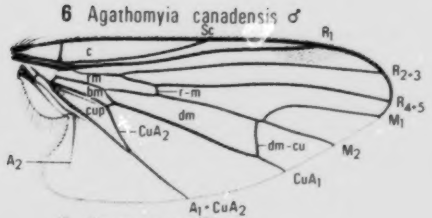
5 Bertamyia notata ♂



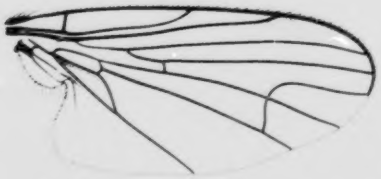
6 Agathomyia canadensis ♂



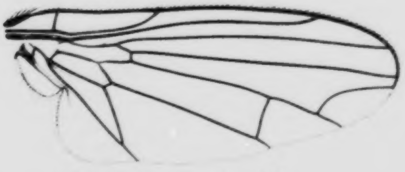
7 Metaclythia currani ♂


Sc
R1
c
hm
bm
cup
r-m
dm
R2+3
R4+5
M1
CuA2
dm-cu
M2
A2
CuA1
A1+CuA2

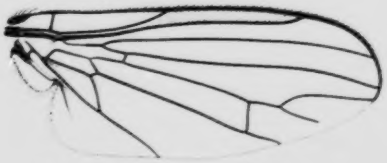
8 Grossoseta pacifica ♂



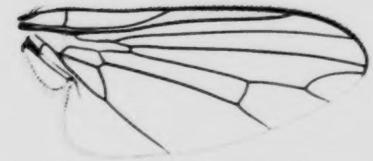
9 Platypezina diversa ♀



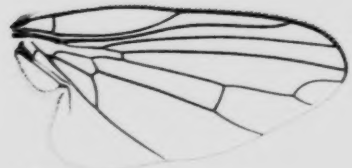
10 Polyporivora polypori ♀



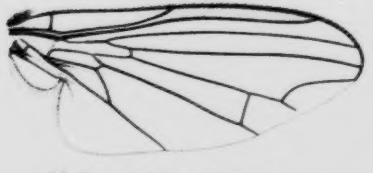
11 Seri dymka ♀



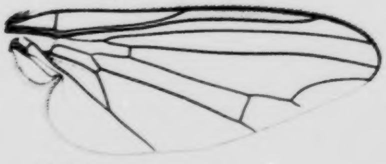
12 Plesioclythia agarici ♂



13 Penesymmetria umbrosa ♂

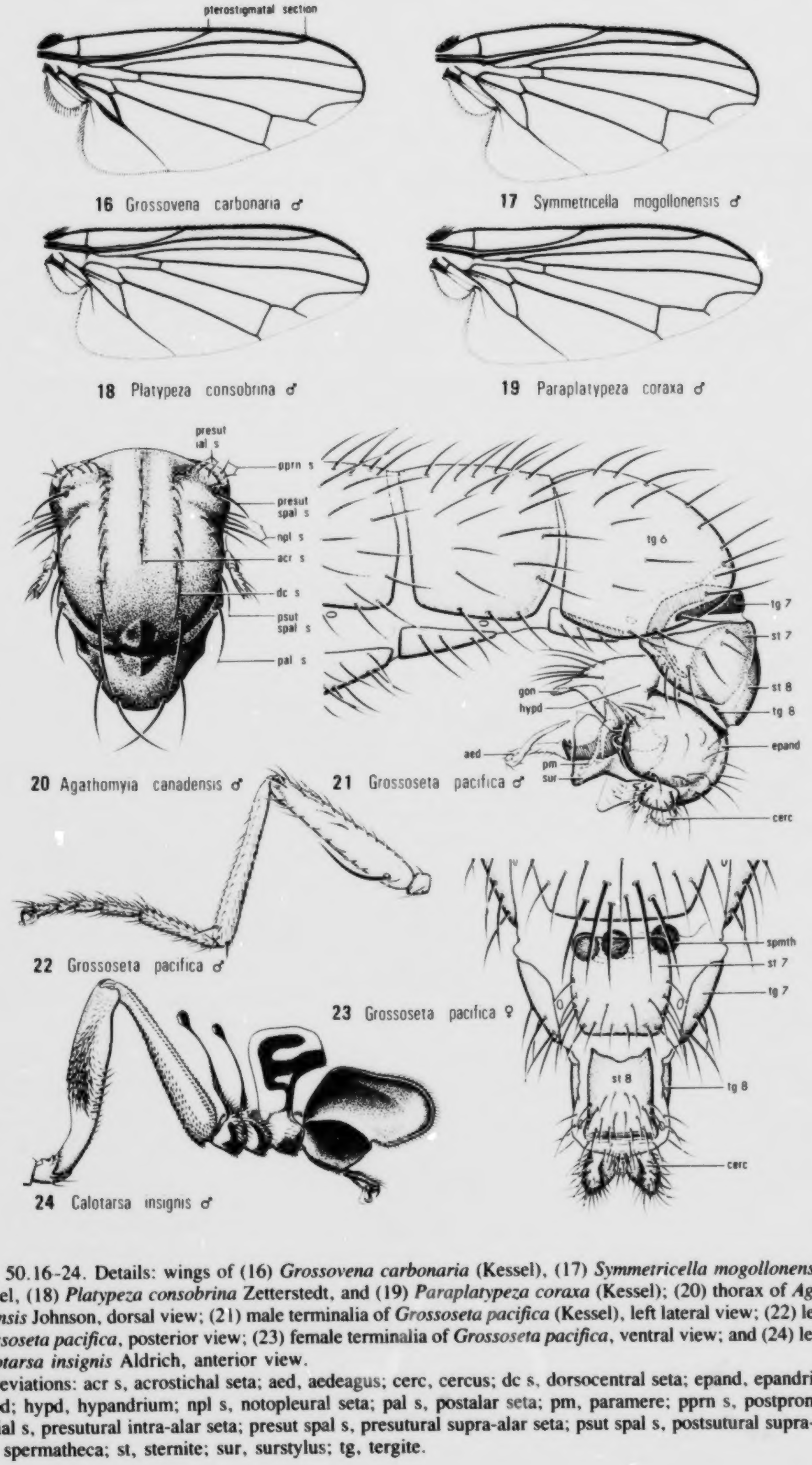


14 Protoclythia modesta ♂



15 Calotarsa insignis ♂

Figs. 50.2–15. Wings: (2) *Melanderomyia* sp.; (3) *Microsania* sp.; (4) *Callomyia calla* Kessel; (5) *Bertamyia notata* (Loew); (6) *Agathomyia canadensis* Johnson; (7) *Metaclythia currani* Kessel; (8) *Grossoseta pacifica* (Kessel); (9) *Platypezina diversa* (Johnson); (10) *Polyporivora polypori* (Willard); (11) *Seri dymka* (Kessel); (12) *Plesioclythia agarici* (Willard); (13) *Penesymmetria umbrosa* (Snow); (14) *Protoclythia modesta* (Zetterstedt) (Palaearctic); and (15) *Calotarsa insignis* Aldrich.


pterostigmatal section
presut ial s
pprn s
presut spal s
npl s
acr s
dc s
psut spal s
pal s
tg 6
tg 7
st 7
st 8
tg 8
gon
hypd
aed
pm
sur
epand
cerc
spmth
st 7
tg 7
st 8
tg 8
cerc

16 Grossovena carbonaria ♂

17 Symmetricella mogollonensis ♂

18 Platypeza consobrina ♂

19 Paraplatypeza coraxa ♂

20 Agathomyia canadensis ♂

21 Grossoseta pacifica ♂

22 Grossoseta pacifica ♂

23 Grossoseta pacifica ♀

24 Calotarsa insignis ♂

Figs. 50.16–24. Details: wings of (16) *Grossovena carbonaria* (Kessel), (17) *Symmetricella mogollonensis* Kessel & Kessel, (18) *Platypeza consobrina* Zetterstedt, and (19) *Paraplatypeza coraxa* (Kessel); (20) thorax of *Agathomyia canadensis* Johnson, dorsal view; (21) male terminalia of *Grossoseta pacifica* (Kessel), left lateral view; (22) left foreleg of *Grossoseta pacifica*, posterior view; (23) female terminalia of *Grossoseta pacifica*, ventral view; and (24) left hindleg of *Calotarsa insignis* Aldrich, anterior view.

Abbreviations: acr s, acrostichal seta; aed, aedeagus; cerc, cercus; dc s, dorsocentral seta; epand, epandrium; gon, gonopod; hypd, hypandrium; npl s, notopleural seta; pal s, postalar seta; pm, paramere; pprn s, postpronotal seta; presut ial s, presutural intra-alar seta; presut spal s, presutural supra-alar seta; psut spal s, postsutural supra-alar seta; spmth, spermatheca; st, sternite; sur, surstylus; tg, tergite.

11. Apical section of M_2 at least three-quarters as long as crossvein dm-cu (Figs. 12, 13) . . 12
Apical section of M_2 at most one-half as long as crossvein dm-cu (Figs. 14–19) 13

12. Cell c symmetric (spearhead-shaped) owing to outward arching of C (Fig. 13) . . . . **Penesymmetria** Kessel & Maggioncalda
3 spp.; southwestern United States; Kessel and Maggioncalda 1968
Cell c asymmetric (scalpel-shaped) owing to inward arching of C (Fig. 12) . . . . **Plesioclythia** Kessel & Maggioncalda
4 spp.; 3 spp. western, 1 sp. eastern; Kessel and Maggioncalda 1968

13. Large fly, 6–10 mm long, predominantly orange yellow in color. Wing venation as in Fig. 15. Hind tarsus of male elaborately ornamented (Fig. 24) . . . . **Calotarsa** Townsend
3 spp.; 2 spp. western, 1 sp. eastern; Kessel 1963
Smaller fly, 2–5 mm long, variable in color. Hind tarsus of male flattened, but not elaborately ornamented 14

14. Cell c symmetric (spearhead-shaped) owing to outward arching of C, and longer than pterostigmatal section (Figs. 16, 17) 15
Cell c asymmetric (scalpel-shaped) owing to inward arching of C, and shorter than pterostigmatal section (Figs. 14, 18, 19) 16

15. Veins bordering cell cup and a contiguous short portion of A_1 grossly thickened in male (Fig. 16). Male terminalia with long filamentous streamers . . . . **Grossovena** Kessel & Maggioncalda
1 sp., *carbonaria* (Kessel); New York to North Carolina, westward to Kansas; Kessel and Maggioncalda 1968
Veins bordering cell cup normal in thickness in both sexes (Fig. 17). Male terminalia without filamentous streamers . . . . **Symmetricella** Kessel
1 sp., *mogollonensis* Kessel & Kessel; New Mexico; Kessel and Maggioncalda 1968

16. Basal tarsomere of posterior tarsus longer than third tarsomere in male, subequal in female. Wing venation as in Fig. 14 . . . . **Protoclythia** Kessel
1 sp., *californica* Kessel; California; Kessel and Maggioncalda 1968
Basal tarsomere of posterior tarsus shorter than third tarsomere in both sexes 17

17. Plane of crossvein r-m crossing near apex of cell c (Fig. 18) . . . . **Platypeza** Meigen
8 spp.; widespread; Kessel and Maggioncalda 1968
Plane of crossvein r-m crossing cell c near apical third (Fig. 19) . . . . **Paraplatypeza** Kessel & Maggioncalda
2 spp.; 1 sp. Pacific Coast, 1 sp. eastern United States; Kessel and Maggioncalda 1968

Larva

1. Marginal processes lacking on all segments . . . . **Agathomyia**
Marginal processes clearly visible on at least last segment (Figs. 25, 27, 29–33) 2

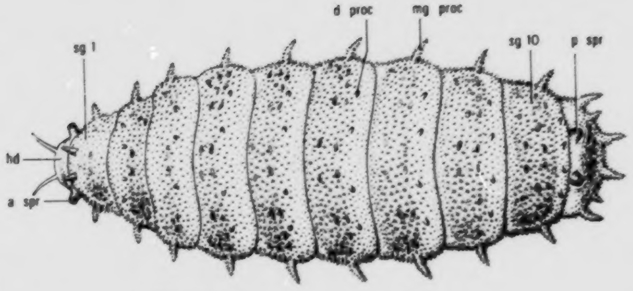
2. Marginal processes scarcely discernible except on last segment (Figs. 27, 29) 3
Marginal processes clearly visible on anterior segments, as well as on last one (Figs. 25, 29–33) 4

3. Body scarcely flattened. Last segment with three pairs of processes; median pair short, fused at their bases (Fig. 27) . . . . **Polyporivora**
Body flattened dorsoventrally. Last segment with two pairs of very small well-separated lateral processes (Fig. 29) . . . . **Melanderomyia**

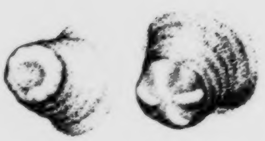
4. Four pairs of marginal processes on last segment (Figs. 31, 32) 5
Three pairs of marginal processes on last segment (Figs. 25, 30, 33) 6

5. Marginal processes ornate, each with conspicuous branched filaments (Fig. 32) . . **Callomyia**
Marginal processes simple (Fig. 31) . . . . **Bertamyia**

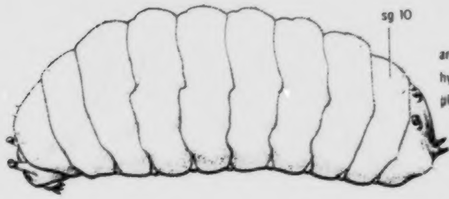
6. Segments 3–10 with two dorsal processes each . . . . **Plesioclythia**
Segments 3–9 with four dorsal processes each (Figs. 25, 30, 33) 7


d proc
mg proc
sg 1
sg 10
p spr
hd
a spr

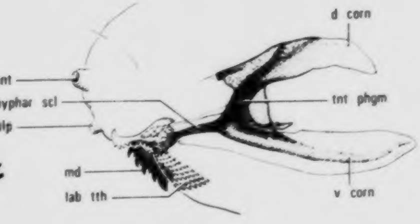
25 Platypeza sp.



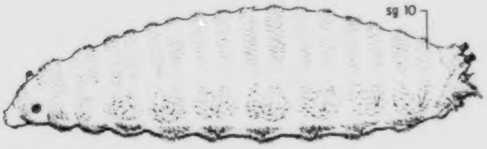
26 Platypeza sp.



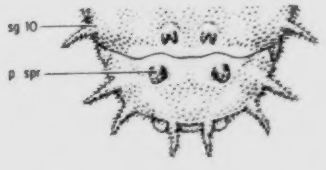
27 Polyporivora polypori


d corn
ant
hyphar scl
plp
tnt phgm
md
lab tth
v corn

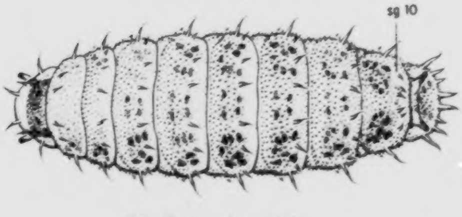
28 Platypeza sp.



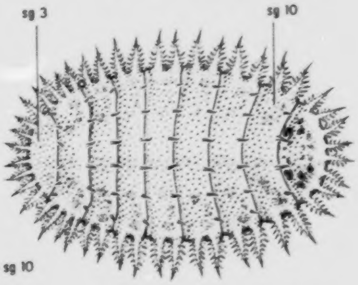
29 Melanderomyia kahli



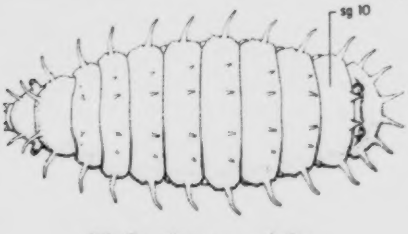
30 Calotarsa insignis



31 Bertamyia notata



32 Callomyia gilloglyorum



33 Paraplatypeza velutina

Figs. 50.25–33. Mature larvae: (25) entire larva of *Platypeza* sp., dorsal view; (26) posterior spiracles of *Platypeza* sp., posterodorsal view; (27) entire larva of *Polyporivora polypori* (Willard), left lateral view; (28) mouthparts of *Platypeza* sp., left lateral view; (29) entire larva of *Melanderomyia kahli* Kessel, left lateral view; (30) apical abdominal segments of *Calotarsa insignis* Aldrich, dorsal view; (31) entire larva of *Bertamyia notata* (Loew), dorsal view; (32) entire larva of *Callomyia gilloglyorum* Kessel, dorsal view; and (33) entire larva of *Paraplatypeza velutina* (Loew), dorsal view.

Abbreviations: ant, antenna; a spr, anterior spiracle; d corn, dorsal cornu; d proc, dorsal process; hd, head; hyphar scl, hypopharyngeal sclerite; lab tth, labial teeth; md, mandible; mg proc, marginal process; plp, palpus; p spr, posterior spiracle; sg, segment; tnt phgm, tentorial phragma; v corn, ventral cornu.

7. Segment 10 with two dorsal processes (Fig. 33) .... ***Paraplatypeza***
Segment 10 with four dorsal processes (Fig. 25, 30) 8

8. Four dorsal processes on segment 10 forming two distinct pairs, each with its members contiguous and arising from a common base (Fig. 30) .... ***Calotarsa***
Four dorsal processes on segment 10 all widely separated as on more anterior segments (Fig. 25) .... ***Platypeza***

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PHORIDAE

51

B. V. PETERSON

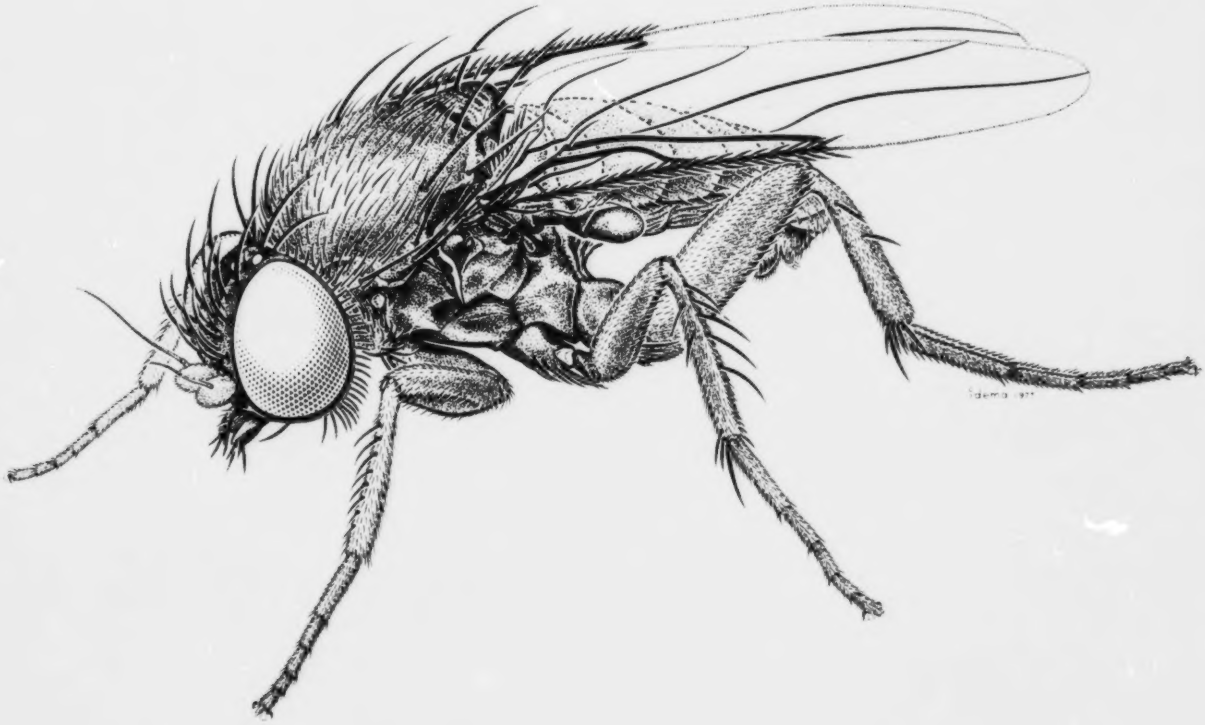
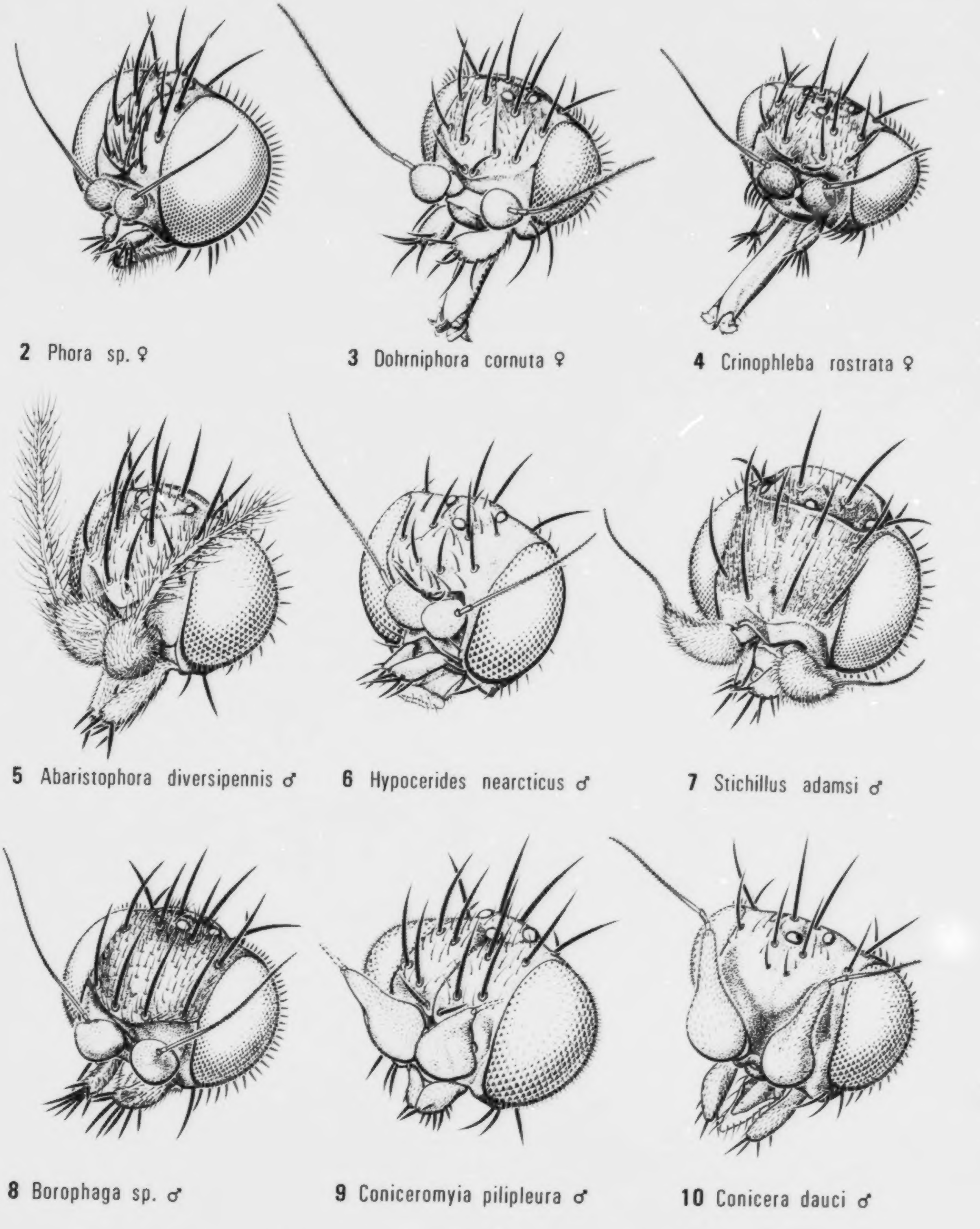


Fig. 51.1. Adult male of *Phora occidentata* Malloch.

Small to minute flies (Fig. 1) about 0.5–5.5 mm long; color blackish, brownish, or yellowish. Thorax often with a characteristic humpbacked appearance. Major bristles of head, legs, and other parts of body characteristically feathered (Fig. 99). Wing (Figs. 41–60) commonly large, usually hyaline to light brown, rarely with dark markings; venation distinctive, with radial veins crowded toward costal margin. Female of some species, however, with wing short or completely absent; some apterous females (Figs. 90, 91, 95, 97) aberrant in form; for example tiny cockroach-like species of *Aenigmatias* Meinert difficult to recognize as Diptera and especially as phorids.

Adult. Head: small, sometimes rather short or flattened (Figs. 2–31). Frons generally wide but varying in length, with or without a median longitudinal furrow (coronal suture); frons and vertex typically with conspicuous bristles arranged in three transverse rows containing four bristles in each (e.g. 4-4-4) (Figs. 18, 19); these bristles sometimes supplemented by additional bristles (e.g. 2-4-4-4, 2-4-6), or reduced in number (e.g. 0-0-6, 0-2-4, 0-2-6, 2-4-4) (bristles reading across from ventral row to dorsal row), and sometimes weak or absent; uppermost row, when complete, consisting of a long inner and a short outer vertical bristle and a pair of long postocellar bristles; two to four strong or weak supra-antennal bristles (sometimes referred to as postantennal bristles), proclinate, porrect, or reclinate, usually present anteromedially just above antennae, sometimes with one or more pairs of supernumerary bristles, or these entirely absent; anterior row of bristles with two middle bristles called lower interfrontal (antial) bristles; presence or absence, position, and direction of inclination of supra-antennal and lower interfrontal bristles taxonomically important. Face short, concave; subcranial cavity large; lower facial margin and clypeus sometimes enlarged and distinctively shaped, especially in female (Figs. 25, 30); proboscis large or small, fleshy and retractile, or produced, sclerotized, and nonretractile (Figs. 3, 4); palpus usually large, often with strong bristles. Eye usually moderately large, but sometimes small especially in brachypterous or wingless



2 Phora sp. ♀

3 Dohrniphora cornuta ♀

4 Crinophleba rostrata ♀

5 Abaristophora diversipennis ♂

6 Hypocerides nearcticus ♂

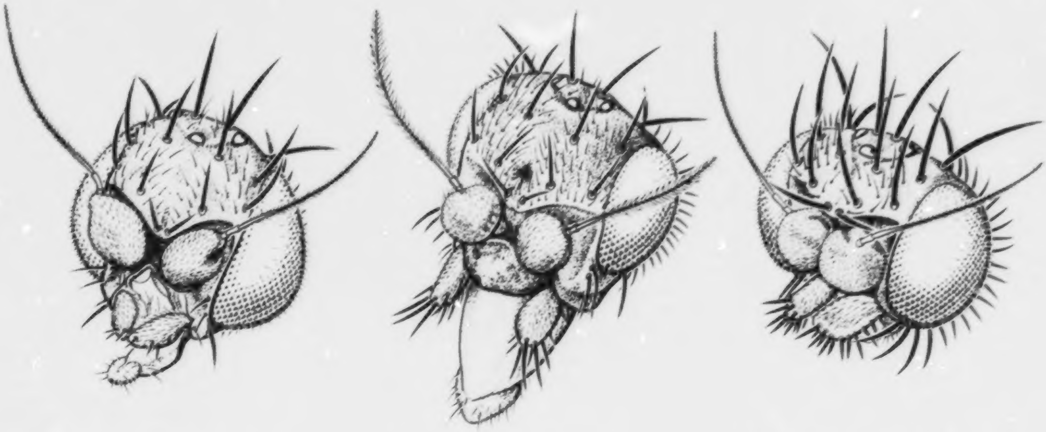
7 Stichillus adamsi ♂

8 Borophaga sp. ♂

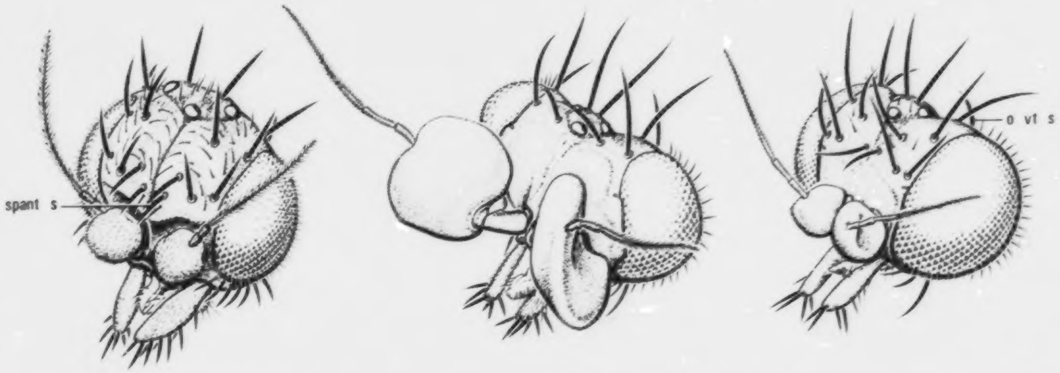
9 Coniceromyia pilipleura ♂

10 Conicera dauci ♂

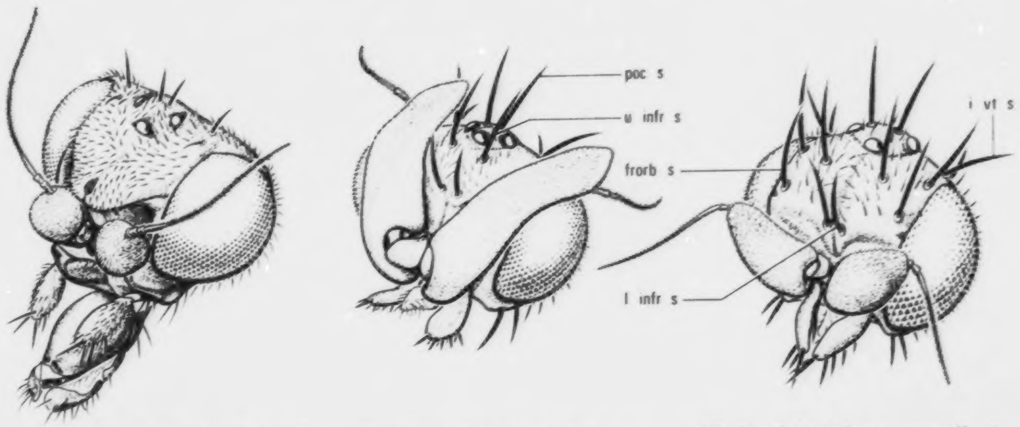
Figs. 51.2–10. Heads: (2) *Phora* sp.; (3) *Dohrniphora cornuta* (Bigot); (4) *Crinophleba rostrata* Borgmeier; (5) *Abaristophora diversipennis* Borgmeier; (6) *Hypocerides nearcticus* Borgmeier; (7) *Stichillus adamsi* (Brues); (8) *Borophaga* sp.; (9) *Coniceromyia pilipleura* Borgmeier; (10) *Conicera dauci* (Meigen) (*continued*).



11 Citrago politifrons ♂ **12** Citrago sp. ♀ **13** Beckerina umbrimargo ♂



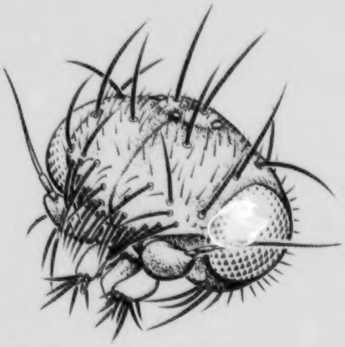
14 Woodiphora magnipalpis ♀ **15** Lecanocerus compressiceps ♂ **16** Lecanocerus compressiceps ♀



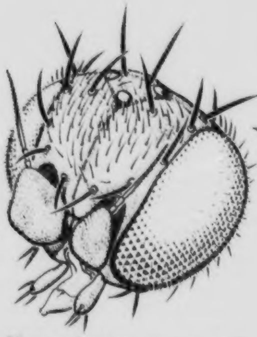
17 Gymnophora luteiventris ♀ **18** Apocephalus wheeleri ♂ **19** Neodohrniphora arnaudi ♂

Figs. 51.11–19. Heads (*continued*): (11) *Citrago politifrons* Borgmeier; (12) *Citrago* sp.; (13) *Beckerina umbrimargo* (Becker); (14) *Woodiphora magnipalpis* (Aldrich); (15) *Lecanocerus compressiceps* Borgmeier, male; (16) *Lecanocerus compressiceps*, female; (17) *Gymnophora luteiventris* Schmitz; (18) *Apocephalus wheeleri* Brues; (19) *Neodohrniphora arnaudi* Borgmeier (*continued*).

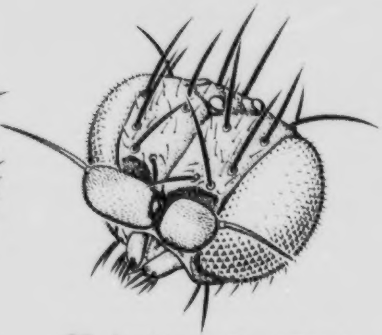
Abbreviations: frorb s, fronto-orbital bristle; i vt s, inner vertical bristle; l infr s, lower interfrontal bristle; o vt s, outer vertical bristle; poc s, postocellar bristle; spant s, supra-antennal bristle; u infr s, upper interfrontal bristle.



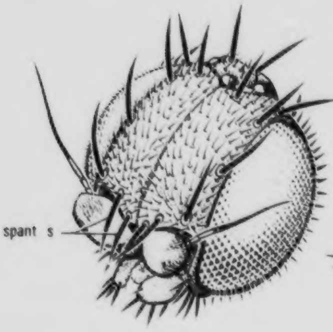
20 Zyziphora hirtifrons ♀



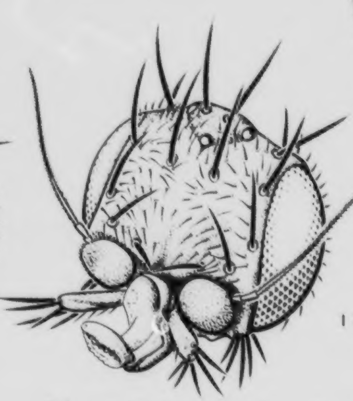
21 Myrmosicarius texanus ♀



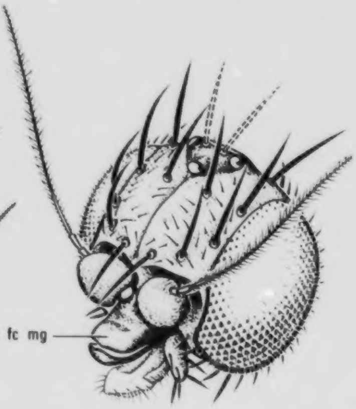
22 Auxanommatidia californica ♂



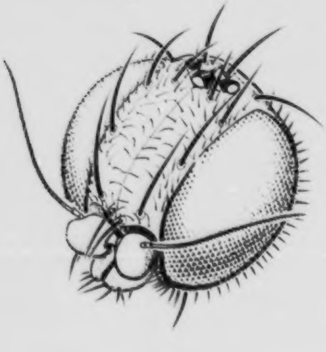
23 Syneura cocciphila ♀



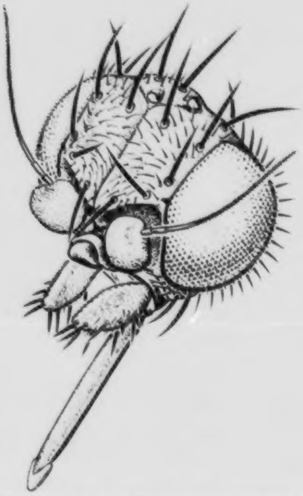
24 Pericyclocera floricola ♀



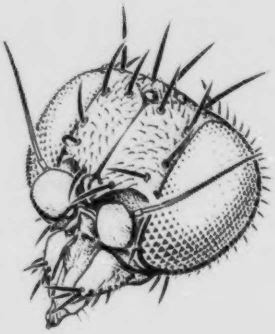
25 Trophithauma rostratum ♀



26 Phalacrotophora longifrons ♀



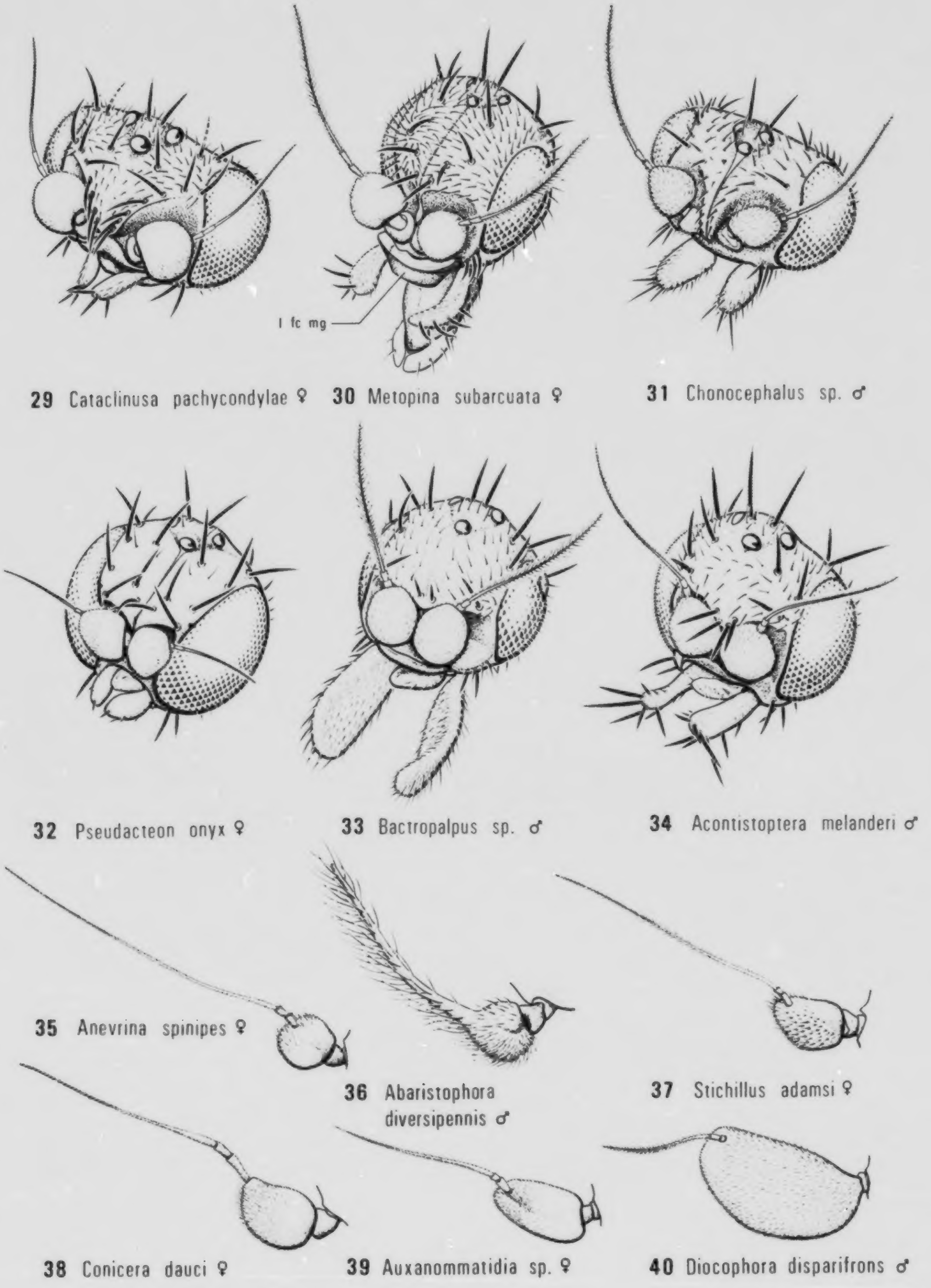
27 Rhyncophoromyia conica ♀



28 Diocophora disparifrons ♀

Figs. 51.20–28. Heads (*continued*): (20) *Zyziphora hirtifrons* Peterson & Robinson; (21) *Myrmosicarius texanus* (Greene); (22) *Auxanommatidia californica* Borgmeier; (23) *Syneura cocciphila* (Coquillett); (24) *Pericyclocera floricola* Borgmeier; (25) *Trophithauma rostratum* (Melander & Brues); (26) *Phalacrotophora longifrons* (Brues); (27) *Rhyncophoromyia conica* (Malloch); (28) *Diocophora disparifrons* Borgmeier (not Nearctic) (*continued*).

Abbreviations: l fc mg, lower facial margin; spant s, supra-antennal bristle.



29 Cataclinusa pachycondylae ♀ **30** Metopina subarcuata ♀ **31** Chonocephalus sp. ♂

32 Pseudacteon onyx ♀ **33** Bactropalpus sp. ♂ **34** Acontistoptera melanderi ♂

35 Anevrina spinipes ♀ **36** Abaristophora diversipennis ♂ **37** Stichillus adamsi ♀

38 Conicera dauci ♀ **39** Auxanommatidia sp. ♀ **40** Diocophora disparifrons ♂

Figs. 51.29–40. Heads (*concluded*) and antennae: head of (29) *Cataclinusa pachycondylae* (Brues), (30) *Metopina subarcuata* Borgmeier, (31) *Chonocephalus* sp., (32) *Pseudacteon onyx* Steyskal, (33) *Bactropalpus* sp., and (34) *Acontistoptera melanderi* Brues; antenna of (35) *Anevrina spinipes* (Coquillett), (36) *Abaristophora diversipennis* Borgmeier, (37) *Stichillus adamsi* (Brues), (38) *Conicera dauci* (Meigen), (39) *Auxanommatidia* sp., and (40) *Diocophora disparifrons* Borgmeier (not Nearctic).

Abbreviation: l fc mg, lower facial margin.

forms, bare or hairy; ocelli usually present, but reduced or absent in some apterous females. Antenna (Figs. 35–40) with scape and pedicel small and sometimes hidden by large first flagellomere; first flagellomere globose, oval, pyriform, conical, or retort-shaped, sometimes greatly enlarged, and sometimes varying in size and shape between sexes; arista apical, subapical, or dorsal in position, rarely absent (*Abaristophora* Schmitz), composed of two basal aristomeres and a long usually more or less pubescent third aristomere.

Thorax: large, usually arched to give a characteristic humpbacked appearance, but sometimes reduced or somewhat flattened. Mesonotum setose, not strongly bristled but usually with one postpronotal, two to four notopleural, one or two supra-alar, and one to three postsutural dorsocentral bristles present; occasionally one presutural and one postsutural intra-alar bristle present; acrostichal setae short but sometimes longer and bristle-like, especially anterior to scutellum; scutellum usually clearly defined but small or absent in some apterous forms, bare or setose above, usually with two to four (zero to six) bristles; anterior pair of scutellar bristles, when present, often weak and hair-like. Proepisternum with or without scattered setae, usually with two to eight ventral and a similar number of dorsal bristles; anepisternum sometimes divided by a dorsoventral anepisternal suture into anterior and posterior parts, bare or setose, sometimes with one or more bristles posterodorsally; remainder of lateral portions of thorax bare.

Legs usually well-developed (Figs. 61–75). Hind femur usually stout, often enlarged, and more or less laterally compressed; various sensory organs sometimes present on inside (posterior) surface at base of hind femur and less frequently on mid femur of male. Tibiae, in addition to one or more apical bristles, with or without strong isolated bristles; often hind tibia, and sometimes mid tibia, with one or two dorsal hair seams composed of short closely set setae (Fig. 63); a row of longer posterodorsal setae also usually present; ctenidia of short setae sometimes present on tibiae and tarsi of midleg and hindleg.

Wing usually large and present in both sexes (Figs. 41–60), but female of some species brachypterous or apterous (Fig. 60). Venation distinctive for family; C strong, extending about half length of wing, sometimes swollen along its entire length or only basally or apically, usually fringed with short to long setae; Sc usually short, free or merged apically or more extensively with R_1, sometimes faint or absent; R_1 and R_{4+5} strong, crowded toward costal margin; Rs simple (R_{4+5}) or with an anterior fork (R_{2+3}), ending in or very near tip of C; remaining veins (M_1, M_2, CuA_1, $A_1 + CuA_2$) thin and weak; M_1 and M_2 often free at base and not directly connected to basal venation of wing. Several tiny pore-like sensory organs not associated with bristles or setae present at various places on anterior veins (Fig. 100); a distributional pattern generally evident, but exact locations and numbers varying considerably; function or taxonomic significance unknown. Halter usually present, but absent in some wingless forms.

Abdomen: well-developed, somewhat conical, and more or less tapered posteriorly, usually with three to six tergites, but often mostly membranous, especially in wingless forms; seven spiracles usually present.

Female of some species with dorsal gland openings on segment 5 or 6; ovipositor small and fleshy (Figs. 76–79); tergite 7 sometimes stiffened by a sclerotized rod; small apparent tergites 9 and 10 sometimes present (Figs. 76–81), or these large, corneous, and adapted for piercing (Figs. 82–85). Single nonsclerotized spermatheca reported by Dufour (1851) and Sturtevant (1925–1926) in three species of two genera of Phoridae.

Male terminalia (Figs. 101–103) small to large in relation to abdomen, usually asymmetric and very complex. Epandrium usually large but sometimes reduced, with one side sometimes more reduced than other side causing variation in shape as well as in size, sometimes simple or with secondary lobes or a secondary process. Surstyli highly variable both in size and shape, often showing considerable variation from side to side, sometimes with one or more secondary lobes or processes; sternite 10 heavily sclerotized, varying in size, shape, and complexity. Epiproct varying from absent or greatly reduced to greatly elongate, usually tube-like (anal tube of authors), and with or without setae; when epiproct developed, cerci demarcated at apex; cerci usually small, but sometimes quite large. Hypandrium variable in size, broadly U-shaped usually, but often asymmetric; usually with a distinct but variably developed aedeagal guide, and sometimes with lobe-like, plate-like, or spiniform processes probably representing gonopods; parameres usually well-developed but varying in size and shape, often complex and asymmetric, often situated in a dorsolateral and ventrolateral position; sperm pump and ejaculatory apodeme, if present, unsclerotized and not discernible; aedeagus correspondingly complex, usually rather short, broad, and mostly membranous; membrane with minute spicules and variously shaped sclerites and often with a variably short to elongate slender subapical spine-like process that may be somewhat membranous or sclerotized; aedeagal apodeme usually short, but often well-developed.

Larva. Small, rarely over 10.0 mm long, typically with 12 visible segments (Fig. 104); shape varying from fusiform with inconspicuous projections on posterior segments to shorter, broader, and somewhat flattened with conspicuous plumose projections dorsally, laterally, and especially on terminal segment; color usually whitish, yellowish white, or grayish. First instar metapneustic, becoming amphipneustic thereafter.

Head or cephalic segment small, inconspicuous, conical, often obliquely truncate ventrally, and often strongly bilobate; small antennal organ and larger ventral lobe-like maxillary palpus present dorsally, both with tiny apical sensilla. A pair of tiny intra-antennal papillae also present dorsally; a transparent vesicle-like labial palpus bearing several tiny papillae and a series of minute setulae present ventromedially; posteroventral margin of head sometimes with a fringe of slender setae, posterior to which is a ventral collar-like series of tiny spinules; lateral portions of head also with tiny spinules. Cephalopharyngeal skeleton (Figs. 106, 107) consisting of a U-shaped tentoropharyngeal sclerite and a median unpaired hook-like labial sclerite; tentoropharyngeal sclerite having narrow dorsal and ventral cornua; labial sclerite lying between reduced or vestigial mandibles and fused to an intermediate hypopharyngeal sclerite.

Thoracic segments bearing near their anterior margins four to six series of posteriorly directed spinules; dorsum of prothorax and dorsal and ventral surfaces of mesothorax often with sclerotized setose areas that are taxonomically important; anterior spiracles small, often situated on tiny projections.

Abdominal segments with various tegumentary and setal formations; some, according to Keilin (1911), metamerically arranged and constant in number, others variable in number, and still others neither metamerically arranged nor constant in number on particular segments; arrangements of these structures often expressed by formulae for taxonomic comparisons. Posterior spiracles (Fig. 105) contiguous or somewhat separated, occurring on well-developed cone-shaped projections situated dorsally on abdominal segment 8 or in a few groups situated terminally on a siphon-like extension of abdominal segment 8; most species with four spiracular openings.

Puparium. Pupation occurring in last larval skin, which hardens and becomes reddish. Puparium (Fig. 108) rather oval, somewhat pointed at ends because larval extremities remain relatively unchanged, convex both dorsally and ventrally, or somewhat convex ventrally and flattened, depressed, or concave dorsally; abdominal segment 2 dorsally with a pair of long slender pupal respiratory organs (horns).

Although several authors have described the immature stages of various phorid species, the best general treatments are those of Keilin (1911), Schmitz (1938–1958), and Hennig (1952).

Biology and behavior. Although the Phoridae, with few exceptions, are among the most easily recognized Diptera, information on the biology of the adults and larvae is scattered and complete life histories are known for only a few species. Robinson (1971) tabulated the biologies of about 170 species of *Megaselia* Rondani and presented an extensive bibliography of papers containing biological information on the Phoridae. A few other recent papers containing important biological information include those of Baumann (1976, 1978), Burges (1979), Disney (1979; 1980*a*, *b*, *c*, and *d*), Disney and Evans (1979), Richardson and Hesling (1977), Robinson (1975), and Robinson and Foote (1968). Adult phorids are usually very active; they have quick, jerky, running-type movements and have been seen swarming in an up-and-down dancing flight. They are found in damp places, on or near many kinds of decomposing plant and animal matter including human corpses, on flowers, fungi, and windows, and in rodent burrows, bird's nests, beehives, wasp and bee nests, ant and termite nests, and caves. The larvae of phorids likewise show many different habitat preferences. In addition to the habitats already mentioned, larvae are known from seed capsules, feces, molluscs and various other gastropods, and many kinds of insects. Some larvae are reported to be internal parasites of various other insects, spiders, and millipedes and others as parasites of, or commensals with, ants or termites. Apparent authentic cases of infestation of wounds, intestines, and eyes of humans by phorid larvae have been recorded (James 1947). Sometimes phorid larvae are of economic importance in the mushroom industry (Robinson 1977). Systematic studies of phorid biologies would be most interesting and rewarding.

Classification and distribution. About 225 genera and over 2500 species of phorids are known in the world fauna (Borgmeier 1968, 1971*b*; Borgmeier and Prado 1975). Nearly half the described species belong to the gigantic and cosmopolitan genus *Megaselia*. The family is divided into six subfamilies, three of which occur in the Nearctic region. Only two tribes are recognized in the current classification, the Beckerinini and Metopinini of the subfamily Metopininae; both tribes are present in our regional fauna. In North America the approximate 356 currently recognized species are scattered among 48 genera.

The higher classification of the Phoridae is reasonably sound, except that the limits of certain genera, especially the *Megaselia*-related group of genera, need more accurate redefinition. The classification of this rather difficult family was placed on a relatively firm basis by Father H. Schmitz with a long series of papers on the subject, especially his *Revision der Phoridae* of 1929, followed by his uncompleted treatment of the Palaearctic species (Schmitz 1938–1958, Schmitz and Beyer 1965). For the Nearctic fauna the papers by Brues are important, especially his works of 1903, 1915, and 1950. Malloch's paper of 1912 is also useful but long out of date. The most significant and useful treatment of North American phorids is found in a series of papers by Borgmeier, especially those of 1963, 1964, 1965, 1968, 1969, 1971*a*, and 1971*b*, which give keys, lists, and descriptions of the North American species.

Forty-two fossil phorid species in 14 genera have been described. Thirty-five of these are from Baltic amber, two are from Zanzibar copal, three are from the Miocene Florissant shales of Colorado, and two are from Canadian Cretaceous amber. The two Canadian species (*Sciadophora bostoni* McAlpine & Martin and *Prioriphora canadambra* McAlpine & Martin) were originally placed in the Sciadoceridae (McAlpine and Martin 1966) but have since been assigned to the Phoridae (Hennig 1973). All but four genera from Baltic amber and the two from Canadian amber are extant genera.

Key to genera*

1. Anterior spiracle dorsal in position (Figs. 87, 88), enclosed by anterodorsal margin of anepisternum which is continuous with curvature of dorsum of thorax. Abdominal segments flattened. Male winged (Fig. 41); female wingless, cockroach-like (Fig. 87). Anepisternum of male with a small posterodorsal subtriangular process that bears a bristle at its apex (Fig. 88) .... AENIGMATIINAE.... ***Aenigmatias*** Meinert

6 spp.; widespread in Canada and northern U.S.A.

Anterior spiracle more lateral in position (Fig. 1), enclosed by anterodorsal margin of anepisternum but this not forming a continuous curvature with dorsum of thorax. Abdominal segments usually arched, not flattened. Both sexes generally winged, but wing sometimes reduced, rudimentary, or absent in female of some species. Anepisternum of male without a posterodorsal subtriangular process 2

2. Tibiae with distinct, though sometimes short or weak, bristles; mid tibia always with at least a closely situated dorsal pair on basal half (Figs. 66, 67); other tibiae sometimes with similar bristles. Wing fully developed in both sexes. Frons bristled along entire lateral margins; supra-antennal bristles, when present, reclinate (Fig. 2) .... PHORINAE.... 3

Tibiae usually without bristles (Figs. 71, 73–75) (except in some *Xanionotum* Brues spp., which have a single anterodorsal bristle very near base on mid and hind tibiae) or with rows of strong setae (Fig. 72). Wing generally fully developed, but sometimes reduced, rudimentary, or absent in female of some species. Frons sometimes bare along margins or on anteroventral half (Fig. 17); supra-antennal bristles variable .... METOPININAE.... 20

3. Rs forked, i.e. R_{2+3} and R_{4+5} present (Fig. 42); R_{4+5} rarely interrupted, except in some species of *Chaetopleurophora* Schmitz 4

Rs not forked, i.e. only R_{4+5} present (Fig. 46) 10

4. Hind tibia with one or two dorsal longitudinal hair seams (Figs. 61, 63) 5

Hind tibia without hair seams (Fig. 65) 6

5. Hind tibia with one hair seam (Fig. 61); hind femur of male with sensory organ consisting of one or more short stout setae at base of posterior (inner) surface (Fig. 62). Anepisternum setose above .... ***Dohrniphora*** Dahl

4 spp.; widespread in U.S.A. and eastern Canada

Hind tibia with two hair seams (Fig. 63); hind femur of male without sensory organ. Anepisternum bare .... ***Diplonevra*** Lioy

5 spp., all in typical subgenus; widespread in U.S.A. and eastern Canada

6. Anepisternum setose, with a long bristle .... ***Chaetopleurophora*** Schmitz

6 spp.; widespread in Canada and U.S.A.

Anepisternum bare 7

7. Rs setose along most of its length (Fig. 43) 8

Rs bare or sparsely setose; if Rs setose, tibial bristles slender and weak 9

8. Proboscis greatly elongated, rigid (Fig. 4). Arista subapical. Scutellum with two strong posterior bristles and two much shorter coarse setae anteriorly. Tergite 6 short. Tibial bristles weak. (Female only; male unknown) .... ***Crinophleba*** Borgmeier

1 sp., *rostrata* Borgmeier; New Brunswick

Proboscis short, broad. Arista clearly dorsal (Fig. 35). Scutellum with four subequal bristles. Tergite 6 of female elongate. Tibial bristles strong (Fig. 65). Terminalia of male large, asymmetric, setose; epiproct short .... ***Anevrina*** Lioy

9 spp.; Alaska, Canada, and northern half of U.S.A.

9. Mid tibia, in addition to a proximal pair of bristles, with a stout anterior bristle some distance from its apex (Fig. 66); all tibial bristles strong. Posterior margin of tergite 8 of female emarginate (Figs. 76, 78) .... ***Spiniphora*** Malloch

5 spp.; widespread in Canada and U.S.A.

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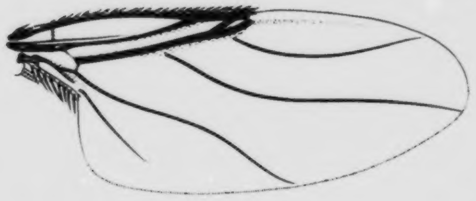
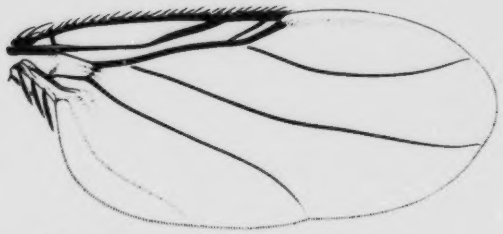
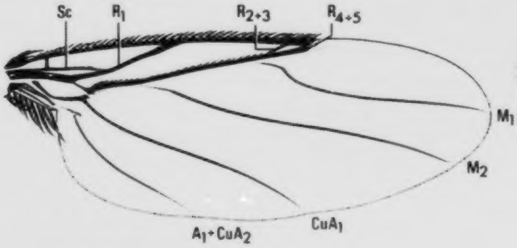
*Note: Long after this manuscript was completed, Disney (1982*a*, J. Zool. Lond. 197: 473–481) reported the genus *Microselia* Schmitz (with *texana* Disney as the only Nearctic species) in North America. Also, Disney (1982*b*, Entomologist's mon. Mag. 118: 247–248) sank *Citrago* Schmitz as a synonym of *Triphleba* Rondani.



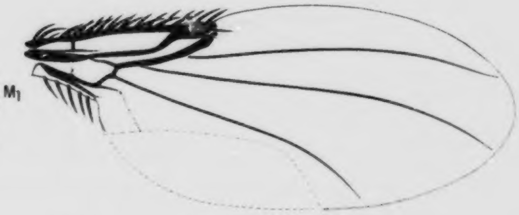
41 Aenigmatias eurynotus ♂



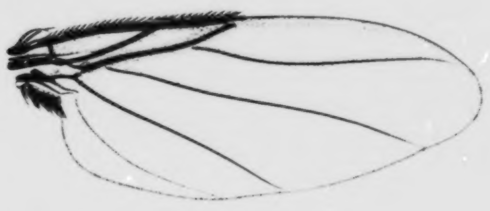
42 Dohrniphora cornuta ♀



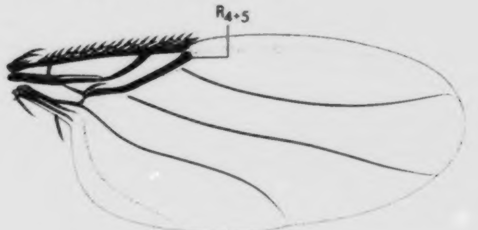
43 Anevrina spinipes ♀



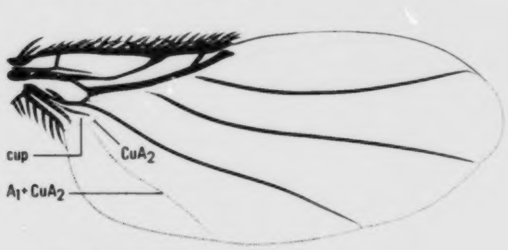
44 Hypocerides nearcticus ♂



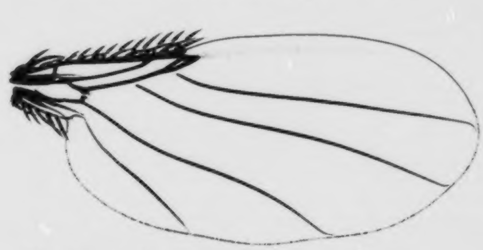
45 Hypocera ehrmanni ♀



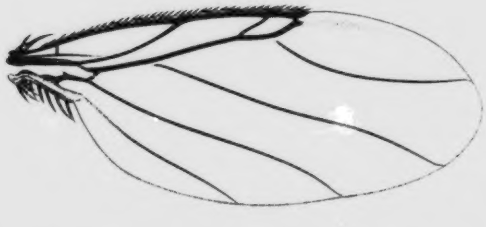
46 Conicera (Hypocerina) sp. ♂



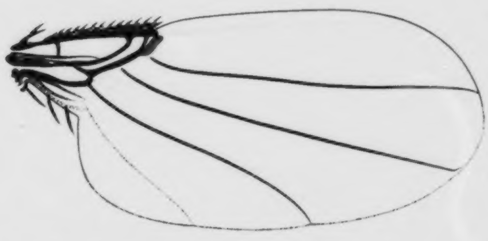
47 Neodohrniphora arnaudi ♂



48 Cremersia spinicosta ♂

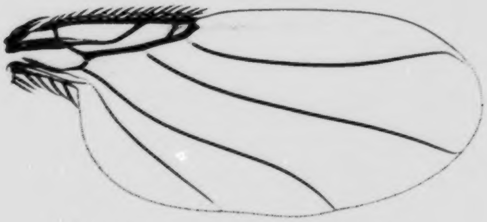


49 Lecanocerus compressiceps ♂

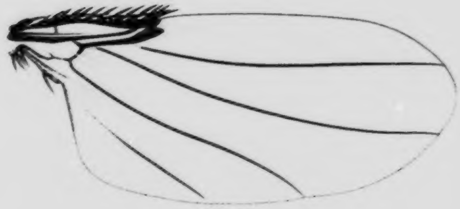


50 Myrmosicarius texanus ♀

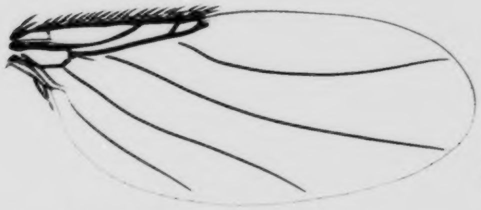
Figs. 51.41–50. Wings: (41) *Aenigmatias eurynotus* (Brues); (42) *Dohrniphora cornuta* (Bigot); (43) *Anevrina spinipes* (Coquillett); (44) *Hypocerides nearcticus* Borgmeier; (45) *Hypocera ehrmanni* Aldrich; (46) *Conicera* (*Hypocerina*) sp.; (47) *Neodohrniphora arnaudi* Borgmeier; (48) *Cremersia spinicosta* (Malloch); (49) *Lecanocerus compressiceps* Borgmeier; (50) *Myrmosicarius texanus* (Greene) (*continued*).



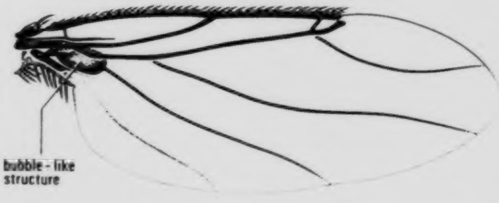
51 Auxanommatidia californica ♂



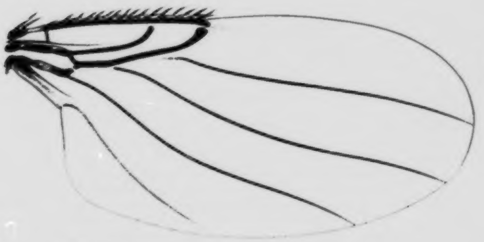
52 Syneura cocciphila ♀



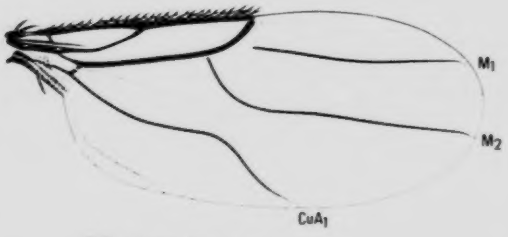
53 Pericyclocera floricola ♀



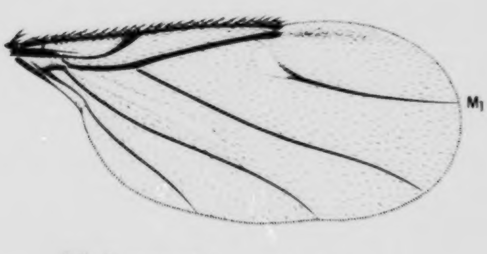
54 Physoptera vesiculata ♀



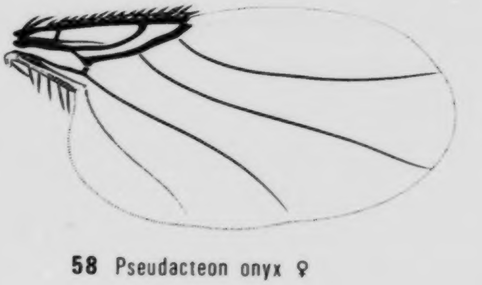
55 Cataclinusa pachycondylae ♂



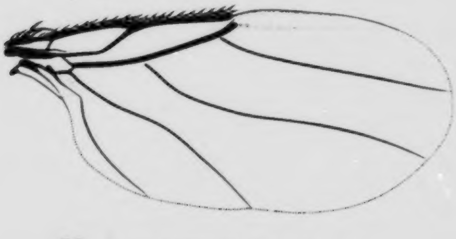
56 Metopina subarcuata ♀



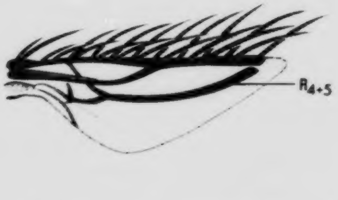
57 Chonocephalus americanus ♂



58 Pseudacteon onyx ♀

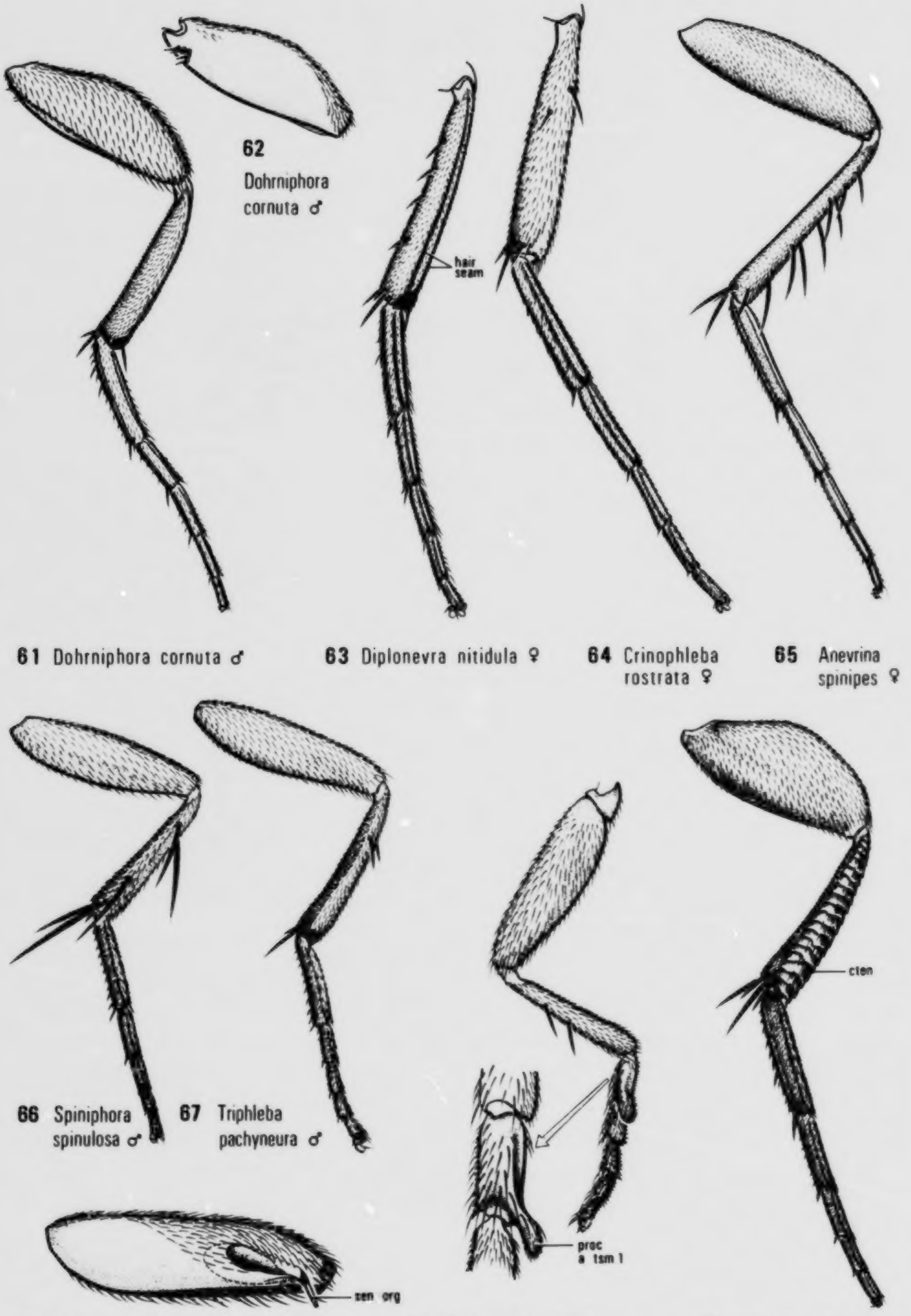


59 Acontistoptera melanderi ♂



60 Commoptera solenopsidis ♀

Figs. 51.51–60. Wings (*concluded*): (51) *Auxanommatidia californica* Borgmeier; (52) *Syneura cocciphila* (Coquillett); (53) *Pericyclocera floricola* Borgmeier; (54) *Physoptera vesiculata* (Borgmeier) (not Nearctic); (55) *Cataclinusa pachycondylae* (Brues); (56) *Metopina subarcuata* Borgmeier; (57) *Chonocephalus americanus* Borgmeier; (58) *Pseudacteon onyx* Steyskal; (59) *Acontistoptera melanderi* Brues; (60) *Commoptera solenopsidis* Brues.



62 Dohrniphora cornuta ♂

61 Dohrniphora cornuta ♂

63 Diplonevra nitidula ♀

64 Crinophleba rostrata ♀

65 Anevrina spinipes ♀

66 Spiniphora spinulosa ♂

67 Triphleba pachyneura ♂

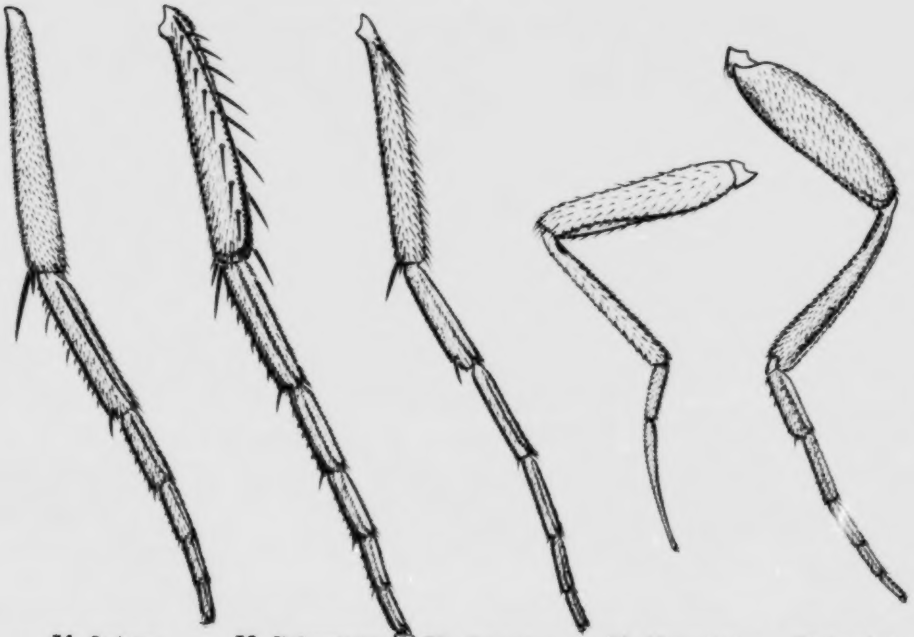
68 Conicera (Tritoconicera) sp. ♂

69 Coniceromyia pilipleura ♂

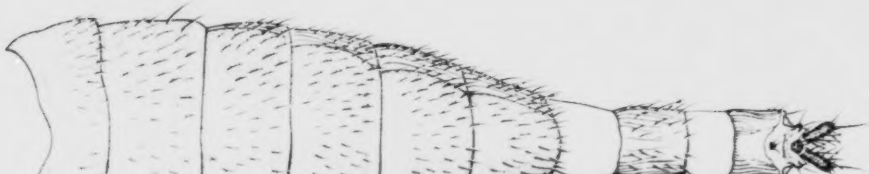
70 Hypocera ehrmanni ♂

Figs. 51.61–70. Legs: (61) anterior view of left hindleg of *Dohrniphora cornuta* (Bigot); (62) posterior view of right hind femur of *Dohrniphora cornuta*; anterior view of left hindleg of (63) *Diplonevra nitidula* Meigen, (64) *Crinophleba rostrata* Borgmeier, and (65) *Anevrina spinipes* (Coquillett); anterior view of left midleg of (66) *Spiniphora spinulosa* (Malloch) and (67) *Triphleba pachyneura* (Loew); (68) posterior view of right mid femur of *Conicera* (*Tritoconicera*) sp.; (69) anterior view of left foreleg of *Coniceromyia pilipleura* Borgmeier; (70) anterior view of left hindleg of *Hypocera ehrmanni* Aldrich (*continued*).

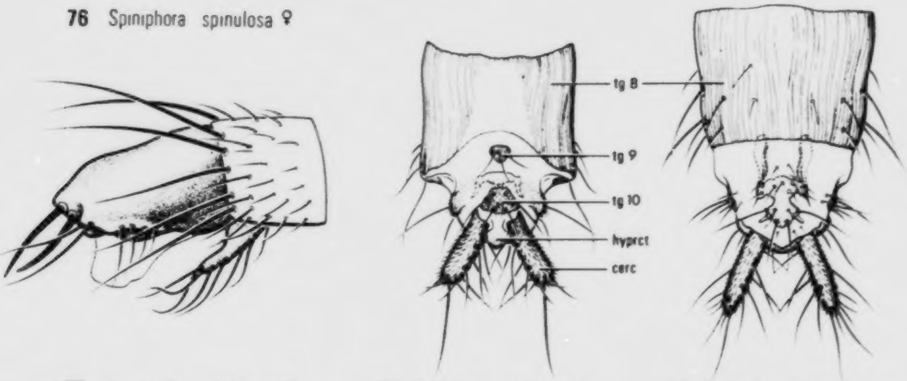
Abbreviations: cten, ctenidium; proc a tsm 1, process of first tarsomere of foreleg; sen org, sensory organ.



71 Beckerina umbrimargo ♀ **72** Phalacrotophora longifrons ♀ **73** Xanionotum mexicanum ♂ **74** Myrmosicarius texanus ♀ **75** Acontistoptera melanderi ♂



76 Spiniphora spinulosa ♀



77 Cremersia spinicosta ♀ **78** Spiniphora spinulosa ♀ **79** Triphleba pachyneura ♀

Figs. 51.71–79. Legs (*concluded*) and abdomens: anterior views of left hindleg of (71) ***Beckerina umbrimargo*** (Becker), (72) ***Phalacrotophora longifrons*** (Brues), and (73) ***Xanionotum mexicanum*** Borgmeier; (74) anterior view of left foreleg of *Myrmosicarius texanus* (Greene); (75) anterior view of left hindleg of *Acontistoptera melanderi* Brues; (76) abdomen of *Spiniphora spinulosa* (Malloch), dorsal view; tip of abdomen of (77) *Cremersia spinicosta* (Malloch) in right lateral view, (78) *Spiniphora spinulosa* in dorsal view, and (79) *Triphleba pachyneura* (Loew) in dorsal view.
Abbreviations: cerc, cercus; hyprct, hypoproct; tg, tergite.

Mid tibia, apart from proximal pair of bristles, with, at most, a weak apical or subapical anterior bristle (Fig. 67); tibial bristles generally weak. Posterior margin of tergite 8 of female not emarginate (Fig. 79) .... ***Triphleba*** Rondani

23 spp.; widespread throughout North America

10. First flagellomere of male globular basally, elongated dorsally into a slender arista-like process bearing long hairs (Figs. 5, 36). Hind tibia with two hair seams. (Male only; female unknown) .... ***Abaristophora*** Schmitz

1 sp., *diversipennis* Borgmeier; Idaho, Montana

First flagellomere not as above; arista normal in both sexes. Hind tibia with or without one or more hair seams 11

11. Fore tibia without bristles on basal half; basal half or more of mid tibia with one to many dorsal bristles in addition to usual basal pair (Fig. 1). Frons with median furrow (Fig. 2). Species black, except for *viridinota* Brues, which is partly greenish .... ***Phora*** Latreille

14 spp.; widespread throughout North America

Fore tibia usually with one or more bristles on basal half; basal half of mid tibia without additional dorsal bristles distal to usual basal pair. Frons with or without median furrow. Species variable in color 12

12. Hind tibia with one or two hair seams 13

Hind tibia without hair seams 15

13. Hind tibia with one hair seam. C and R_{4+5} joining apically in a pterostigma-like swelling (Fig. 44). Two weak supra-antennal bristles present (Fig. 6). Anepisternum bare .... ***Hypocerides*** Schmitz

1 sp., *nearcticus* Borgmeier; Virginia

Hind tibia with two hair seams. Junction of apex of C and R_{4+5} simple, without a pterostigma-like swelling. Supra-antennal bristles absent (Fig. 8). Anepisternum setose 14

14. Ocelli widely separated; lateral ocelli situated close to eye margins; ocellar triangle separated from frons by an indented line forming three variably accentuated loops (Fig. 7). First flagellomere oval, pyriform, or conical (Fig. 37) .... ***Stichillus*** Enderlein

5 spp.; mostly in southern U.S.A.

Ocelli situated normally near center of vertex; ocellar triangle not separated from frons by a looped line. First flagellomere globose (Fig. 8) .... ***Borophaga*** Enderlein

5 spp., all in typical subgenus; widespread throughout North America

15. Anepisternum setose, often with a long bristle. Frons with or without a median furrow 16

Anepisternum bare. Frons without a median furrow 17

16. Anepisternum with a long stout bristle. Frons without a median furrow. Arista dorsal. Alular area of wing with numerous bristles (Fig. 45). Tarsomere 1 of fore tarsus of male simple; mid and hind tibiae of both sexes with ctenidia (Fig. 70) .... ***Hypocera*** Lioy

2 spp.; California to Connecticut and Ontario

Anepisternum with fine setae only, without a long bristle. Frons with a median furrow (Fig. 9). Arista apical, rarely subapical. Alular area of wing with one bristle. Tarsomere 1 of fore tarsus of male with a slender fringed process at apex (Fig. 69); mid and hind tibiae of both sexes without ctenidia .... ***Coniceromyia*** Borgmeier

2 spp.; Arizona, Texas to Florida

17. Hind tibia without a closely placed pair of basal bristles, at most with one or two solitary bristles on distal half. Proboscis of female thick and sclerotized (Fig. 12). First flagellomere of male subconical, pointed apically (Fig. 11); this flagellomere in female of known species globose .... ***Citrago*** Schmitz

2 spp.; Minnesota, Massachusetts

Hind tibia with a closely placed pair of basal bristles. Proboscis of female normal. First flagellomere of male large, conical or retort-shaped (Fig. 10); this flagellomere in female globose, with pointed apex (Fig. 38) .... ***Conicera*** Meigen 18

18. Rs with a short bristle at base in both sexes (Fig. 46). Right surstylus of male terminalia with a somewhat medially directed, variably sized plate or peg-shaped process on inner margin (Fig. 101) .... ***Conicera*** (***Hypocerina*** Malloch)

2 spp.; western and eastern U.S.A.

Rs without a bristle at base. Male terminalia not as above 19

19. Supra-antennal bristles present in both sexes. CuA$_1$ and A$_1$ + CuA$_2$ not reaching hind margin of wing. Apex of inner surface of mid femur of male with a sense organ apparent externally as a fovea and a hollow tube-like spur (Fig. 68) ..... ***Conicera*** (***Tritoconicera*** Schmitz)
3 spp.; California, Montana to New York

Supra-antennal bristles absent in male; anterolateral bristles absent in both sexes. CuA$_1$ and A$_1$ + CuA$_2$ reaching hind margin of wing. Mid femur of male without a sense organ .. .. ***Conicera*** (***Conicera*** Meigen)
1 sp., *dauci* (Meigen); widespread in Canada and U.S.A.

20. Frons with two to four strongly divergent supra-antennal bristles; these bristles more or less reclinate or porrect, rarely slightly proclinate (Fig. 13). Tibiae without bristles and without a posterodorsal row of setae (Fig. 71) (one species, *aliena* Malloch, with a hair seam on hind tibia but without a row of strong posterodorsal setae). Rs forked .... METOPININAE, BECKERININI .... ***Beckerina*** Malloch
5 spp.; widespread throughout North America

Frons with supra-antennal bristles proclinate or absent; when present, these bristles not strongly divergent. (Female of *Lecanocerus* with moderately diverging supra-antennal bristles (Fig. 16); mid and hind tibiae with hair seam and often with strong posterodorsal setae.) Rs forked or simple .... METOPININAE, METOPININI 21

21. Wing fully developed (all males, some females) 22

Wing considerably reduced, rudimentary, or absent (females only) 64

22. Rs usually forked, but in some genera, e.g. *Syneura*,[1] anterior branch of fork (R_{2+3}) sometimes weakened or faint 23

Rs not forked 51

23. Hind tibia without a hair seam and without posterodorsal setae, bare except for normal decumbent basic pubescence and possibly some erect posteroventral hairs 24

Hind tibia with a hair seam and with posterodorsal setae; setae sometimes weak 25

24. Anterior margin of frons rounded, projecting over bases of antennae; anteroventral half of frons without bristles, but often with four to six weak bristles near dorsal margin of vertex; median furrow absent or rudimentary (Fig. 17). Anepisternum with a few setae dorsally. Body practically destitute of bristles .... ***Gymnophora*** Macquart
3 spp., all in typical subgenus; widespread throughout North America

Anterior margin of frons normal, not rounded nor projecting over bases of antennae; frons and vertex normally bristled, with three rows of four bristles each (4-4-4); median furrow present (Fig. 14). Anepisternum bare. Body more normally bristled .. ***Woodiphora*** Schmitz
1 sp., *magnipalpis* (Aldrich), in typical subgenus; Missouri

25. Supra-antennal bristles absent; their place sometimes occupied by parallel or divergent lower interfrontal bristles (Figs. 15, 18, 19) 26

Supra-antennal bristles present, represented by at least one pair, variably directed (Figs. 20, 21, 23) 30

26. C slightly but distinctly thickened along its entire length; Sc present and distinct; M$_1$ concave, recurved posteriorly near apex; bases of M$_1$ and M$_2$ not closely approximated (Fig. 47). Male terminalia moderately large; epiproct moderately long, broad, and tapering to a sharp point, with strong apical hairs. (Male only; female of North American species unknown)..... .... ***Neodohrniphora*** Malloch[2]
1 sp., *arnaudi* Borgmeier; California

C normal or not thickened along its entire length; Sc present but sometimes indistinct; M$_1$ more or less straight or not noticeably concave; if M$_1$ recurved posteriorly near apex, then bases of M$_1$ and M$_2$ rather closely approximated (Fig. 48). Male terminalia small or large, but if large, then strongly asymmetric. Female with sclerotized ovipositor of various forms 27

27. Bases of M$_1$ and M$_2$ closely approximated; Sc indistinct; C with moderately long setae (Fig. 48). Ovipositor of female asymmetric, complicated, variable in shape (Fig. 77). Male ter-

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[1] This genus is run through both parts of couplet 22 because fork of Rs is sometimes so faint that it is not readily discernible.

[2] According to Borgmeier (1965) the North American species assigned to *Neodohrniphora*, "... differs so strikingly from the other two (Neotropical species) that one may doubt if it really belongs here or if it is not better made the type of a new genus. The female is necessary to decide this question."

minalia asymmetric; right side of epandrium much reduced, with a large cavity (Fig. 102) .... ***Cremersia*** Schmitz

3 spp.; Texas

Bases of M_1 and M_2 not closely approximated; Sc distinct; C with short setae (Fig. 49). Ovipositor of female symmetric, even though variable in shape (Fig. 83). Male terminalia small 28

28. Head strongly compressed from front to back; frons very short; median furrow present but weakly defined and difficult to discern. Supra-antennal bristles absent; only two transverse rows of four bristles each (0-4-4) on frons and vertex; upper interfrontal (preocellar) bristles usually converging. First flagellomere very large, rounded, dish-like, excavated laterally (Fig. 15). (Male only; for female see couplet 38) .... ***Lecanocerus*** Borgmeier, in part

1 sp., *compressiceps* Borgmeier; eastern Canada, U.S.A.

Head normal, not strongly compressed from front to back; frons not very short; median furrow distinct. Three transverse rows of bristles (2-2-4, 4-4-4) present on frons and vertex; rarely an apparent fourth row (2-2-4-4) also evident. First flagellomere oval or conical; that of male often greatly enlarged .... ***Apocephalus*** Coquillett, in part 29

29. Male with bristles of frons and vertex arranged 2-2-4; those of female arranged 2-4-4 or apparently 2-2-4-4 (actually 4-4-4 but anterior fronto-orbital bristles situated anteriorly near midline). First flagellomere enlarged, often considerably so in male (Fig. 18), but of normal size in both sexes of *borealis* Brues .... ***Apocephalus*** (***Mesophora*** Borgmeier)

4 spp.; British Columbia, widespread in U.S.A.

Bristles on frons and vertex arranged in three rows of 4-4-4. First flagellomere normal, not enlarged in either sex .... ***Apocephalus*** (***Apocephalus*** Coquillett)

14 spp.; widespread in U.S.A. and eastern Canada

30. Frons with a group of eight to ten supra-antennal bristles on each side of median furrow (Fig. 20). (Female only; male unknown) .... ***Zyziphora*** Peterson & Robinson

1 sp., *hirtifrons* Peterson & Robinson, Colorado

Frons with one or two pairs of supra-antennal bristles 31

31. Lower interfrontal bristles close together near median line, at least weakly divergent (Fig. 18) .... ***Apocephalus*** Coquillett, in part

see couplet 29

Lower interfrontal bristles convergent or parallel, variable in position 32

32. First flagellomere of either sex conical or pear-shaped; arista apical or subapical 33

First flagellomere of both sexes roundish or oval; position of arista variable 36

33. Anepisternum setose, with a single large bristle. (Male only; male of North American species not known; for female see couplet 46) .... ***Diocophora*** Borgmeier, in part

2 spp.; New York, Florida

Anepisternum bare 34

34. Lower interfrontal bristles parallel or slightly divergent, situated close together near midline of frons, or if more distant from each other, then not vertically below anterior fronto-orbital bristles. Ommatidia of eye uniform in size .... ***Apocephalus*** Coquillett, in part

see couplet 29

Lower interfrontal bristles convergent, situated near anterior corners of frons nearly vertically below anterior fronto-orbital bristles. Ommatidia of eye increasing in size ventrally (Fig. 22) 35

35. Fore tarsus with two tarsomeres (tarsomeres 2–5 fused), with apical tarsomere long, thin, and pointed; claw rudimentary (Fig. 74). M_1 only slightly concave, arising at base of fork of Rs; this fork very narrow and indistinct (Fig. 50). (Female only; male of North American species unknown) .... ***Myrmosicarius*** Borgmeier

1 sp., *texanus* (Greene); Texas

Fore tarsus of both sexes with the usual five tarsomeres, although apical tarsomere in female sometimes thin and pointed; claw normal. M_1 slightly concave on basal half, recurved at tip, and arising near middle of fork of Rs; this fork narrow but distinct (Fig. 51) .... ***Auxanommatidia*** Borgmeier

1 sp., *californica* Borgmeier; California

36. Sc weakly developed or indistinctly evident (Figs. 52, 53) 37

Sc well-developed or clearly evident 38

37. Anepisternum setose. R_1 and R_{4+5} approximated apically; fork of Rs faintly indicated; bases of M_1 and M_2 approximated basally (Fig. 52). Lower facial margin of female normal, not enlarged nor separating antennal cavities .... ***Syneura*** Brues, in part

1 sp., *cocciphila* (Coquillett); Texas

Anepisternum bare. R_1 and R_{4+5} not approximated apically; fork of Rs distinct; bases of M_1 and M_2 separated basally (Fig. 53). Lower facial margin of female somewhat enlarged, apparently separating antennal cavities (Fig. 24). (Female only; male unknown) .... ***Pericyclocera*** Schmitz, in part

1 sp., *floricola* Borgmeier; California

38. Head moderately but noticeably shortened; antennal cavities weakly developed, almost flat; one pair of slightly proclinate and moderately divergent supra-antennal bristles present; these bristles about as long and stout as other major bristles on frons. First flagellomere roundish, but lateral surface flattened and median surface convex (Fig. 16). Ovipositor sclerotized, broad basally, pointed apically. (Female only; for male see couplet 28) .... ***Lecanocerus*** Borgmeier, in part

see couplet 28

Head variable but not noticeably shortened; antennal cavities usually well-developed and deep, but sometimes variable; one or two pairs of distinctly proclinate and less divergent supra-antennal bristles present; these bristles usually shorter and weaker than other major bristles on frons. First flagellomere usually more globose or oval. Ovipositor of female variable 39

39. Female 40

Male 49

40. Proboscis long, slender, sclerotized, rigid, pointed apically, geniculate at base (Fig. 27) ... . ***Rhyncophoromyia*** Malloch, in part

2 spp.; eastern U.S.A.

Proboscis not strikingly long and slender but short and often stout, and if sclerotized at least somewhat retractile 41

41. Rs with a bubble-like modification basally (Fig. 54) .... ***Physoptera*** Borgmeier, in part

2 spp.; eastern U.S.A.

Rs without a bubble-like modification at base 42

42. Lower margin of face conspicuously produced as a shiny half-tube or roof-like structure; proboscis stout, composed of partly separated clypeus and labium (Fig. 25) .... ***Trophithauma*** Schmitz, in part

1 sp., *rostratum* (Melander & Brues); eastern U.S.A.

Lower margin of face sometimes swollen, but not produced as a half-tube or roof-like structure; proboscis normal 43

43. Lower margin of face enlarged, separating antennal grooves; ventral side excavated for reception of short stout proboscis. Anepisternum setose, with one long bristle .... ***Pericyclocera*** Schmitz, in part

1 sp., *cata* (Melander & Brues); Massachusetts

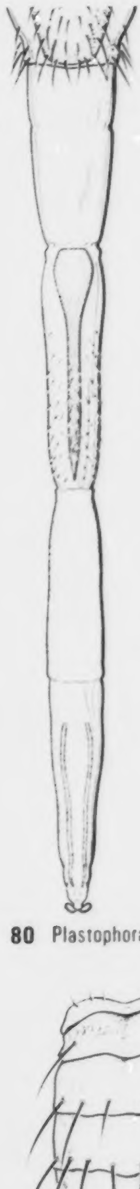
Lower margin of face normal or only slightly swollen; antennal grooves clearly merging, at most only weakly or partially separated. Anepisternum bare or setose 44

44. Frons always clearly longer than wide, with sides parallel, and often shining; lower interfrontal bristles parallel to slightly divergent, arising near anterior margin of frons far below anterior fronto-orbital bristles (Fig. 26). Mid and hind tibiae with a row of strong setae on each side of hair seam (Fig. 72) .... ***Phalacrotophora*** Enderlein, in part 45

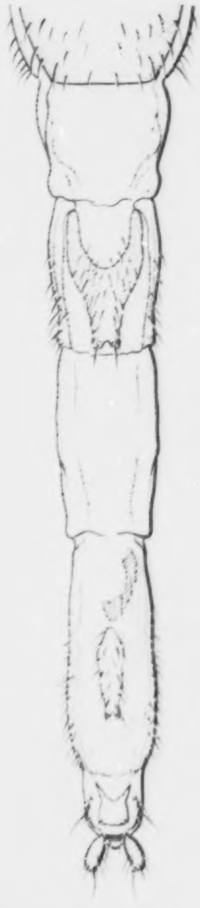
Frons usually wider than long; if frons longer than wide, lower interfrontal bristles usually convergent, not arising near anterior margin of frons nor at a considerable distance below anterior fronto-orbital bristles. Mid and hind tibiae usually with only a posterodorsal row of setae; if an anterodorsal row present, these setae weak 46

45. Anepisternum setose, often with one or two long bristles .... ***Phalacrotophora*** (***Phalacrotophora*** Enderlein), in part

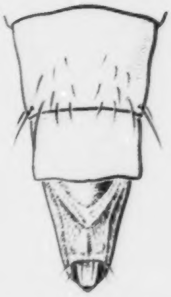
2 spp.; Ontario, California to New York



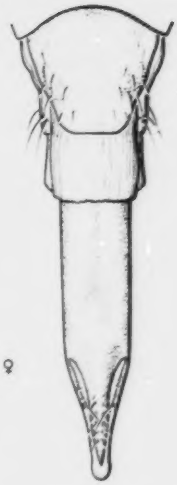
80 Plastophora sp. ♀



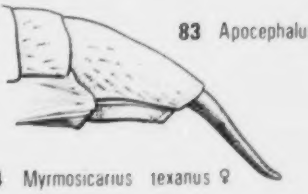
81 Megaselia iroquoiana ♀



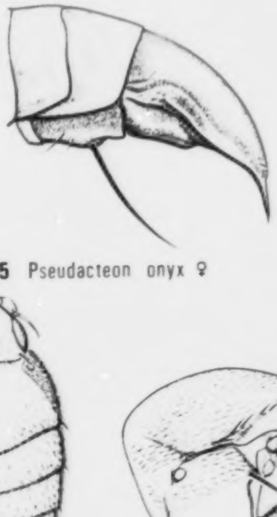
82 Diocophora disparifrons ♀



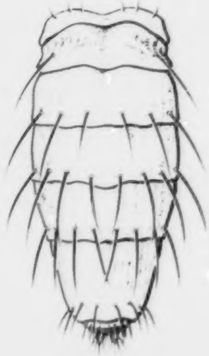
83 Apocephalus wheeleri ♀



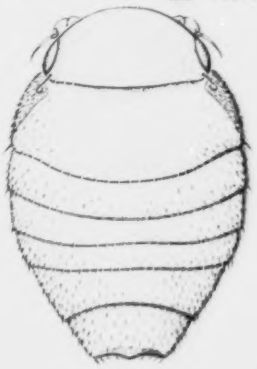
84 Myrmosicarius texanus ♀



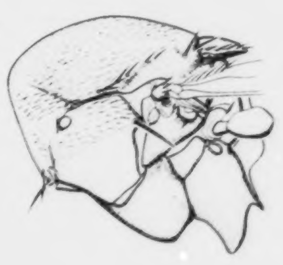
85 Pseudacteon onyx ♀



86 Xanionotum sp. ♀



87 Aenigmatias eurynotus ♀



88 Aenigmatias eurynotus ♂

Figs. 51.80–88. Abdomens, habitus, and thorax: dorsal views of ovipositor of (80) *Plastophora* sp., (81) *Megaselia iroquoiana* (Malloch), (82) *Diocophora disparifrons* Borgmeier (not Nearctic), and (83) *Apocephalus wheeleri* Brues; left lateral views of ovipositor of (84) *Myrmosicarius texanus* (Greene) and (85) *Pseudacteon onyx* Steyskal; (86) dorsal view of abdomen of *Xanionotum* sp.; (87) dorsal view of habitus of *Aenigmatias eurynotus* (Brues); (88) left lateral view of thorax of *Aenigmatias eurynotus*.

Anepisternum bare .... ***Phalacrotophora*** **(*Omapanta*** Schmitz), in part
1 sp., *longifrons* (Brues); Ontario, eastern U.S.A.

46. Frons pentagonal; anterior margin somewhat pointed medially. Clypeus slightly enlarged and protruding. Proboscis stout and sclerotized; palpus rather triangular (Fig. 28). Anepisternum setose, with a single bristle. Venter of abdomen often with long bristles; ovipositor slightly sclerotized, somewhat flattened; cerci absent (Fig. 82). (For male see couplet 33).... .... ***Diocophora*** Borgmeier, in part
see couplet 33

Not agreeing with above combination of characters 47

47. Ovipositor at least slightly sclerotized or horny, sometimes stylet-shaped; cerci small or absent (Fig. 80). Lower interfrontal bristles usually removed from margins of eyes, reclinate, and somewhat parallel. Arista usually short, often not longer than frons .... ***Plastophora*** Brues, in part[3]
8 spp.; widespread in Canada and U.S.A.

Ovipositor of female usually more fleshy, of normal form; cerci present, variable in size, generally directed ventrally (Fig. 81). Lower interfrontal bristles usually inclined toward median line and variable in position. Arista variable but usually longer than frons .... ***Megaselia*** Rondani, in part.... 48

48. Anepisternum bare .... ***Megaselia*** **(*Megaselia*** Rondani), in part
about 76 spp.; widespread in Canada and U.S.A.

Anepisternum hairy, sometimes with bristles .... ***Megaselia*** **(*Aphiochaeta*** Brues)
about 101 spp.; widespread in Canada and U.S.A.

49. Frons always clearly longer than wide, with sides parallel, and often shining; lower interfrontal bristles parallel to slightly divergent, arising near anterior margin of frons far below anterior fronto-orbital bristles (Fig. 26). Mid and hind tibiae with a row of strong setae on each side of hair seam (Fig. 72) .... ***Phalacrotophora*** Enderlein, in part.... 50
see couplet 45

Not agreeing with above combination of characters[4] .... ***Megaselia*** Rondani, in part
see couplet 48

.... ***Pericyclocera*** Schmitz, in part
see couplet 43

.... ***Physoptera*** Borgmeier, in part
see couplet 41

.... ***Plastophora*** Brues, in part[3]
see couplet 47

.... ***Rhyncophoromyia*** Malloch, in part
see couplet 40

.... ***Trophithauma*** Schmitz, in part
see couplet 42

50. Anepisternum setose, often with one or two long bristles .... ***Phalacrotophora*** Enderlein, in part
see couplet 45

Anepisternum bare .... ***Phalacrotophora*** **(*Omapanta*** Schmitz), in part
see couplet 45

51. Frons and vertex with 12 major bristles arranged in three transverse rows containing four bristles each (4-4-4) 52

Frons and vertex with fewer (0-0-6, 0-2-4, 0-2-6, 2-4-4) or more (2-4-4-4) than 12 major bristles; if 12 bristles present (rarely), these arranged 2-4-6 but never 4-4-4 54

52. Frons more or less pentagonal, narrowed anteriorly, with median prolongation nearly touching lower margin of face; median furrow absent (Fig. 29). Apex of C turned posteriorly toward

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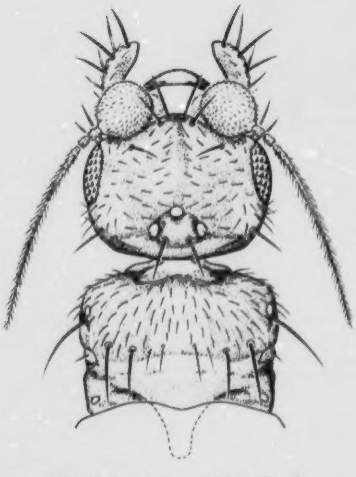
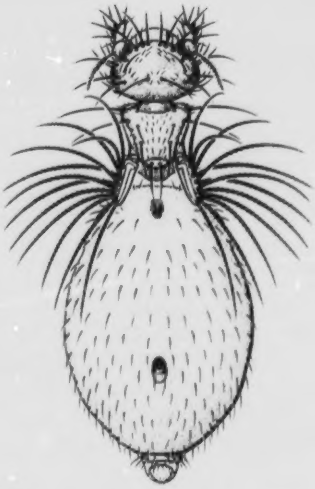
[3] According to Disney (1978), "The definition of the genus *Plastophora* has become so obscured... that it is no longer possible to cite characters that would definitely distinguish most species from *Megaselia*... The case for retaining the genus *Plastophora* at all is virtually indefensible." The genus *Plastophora* is provisionally included in the key pending a final judgement on its validity.

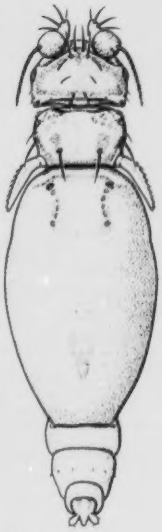
[4] Reliable characters for separating males of these six tentative genera are not known.



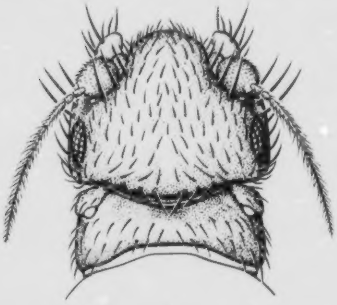
89 Puliciphora occidentalis ♀



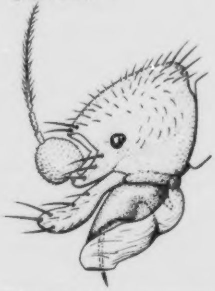
90 Acontistoptera brasiliensis ♀



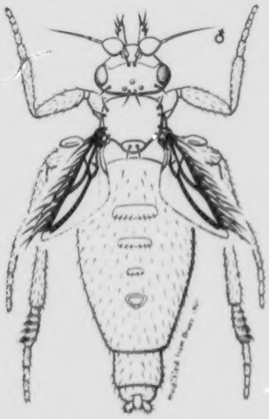
91 Ecitomyia wheeleri ♀



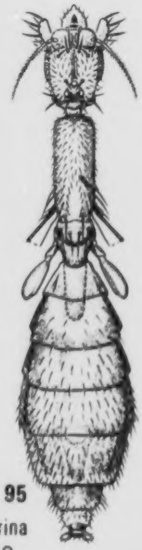
92 Chonocephalus sp. ♀



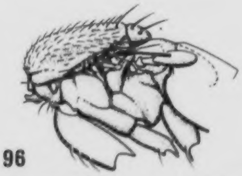
93 Trophodeinus pygmaeus ♀



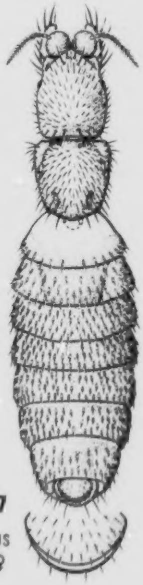
94 Commoptera solenopsidis ♀



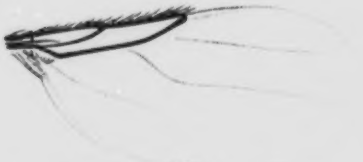
95 Stenophorina petiolata ♀



96 Stenophorina petiolata ♀



97 Trophodeinus pygmaeus ♀



98 Stenophorina petiolata ♀

Figs. 51.89–98. Heads, thoraces, habitus, and wing: (89) head and thorax of *Puliciphora occidentalis* (Melander & Brues); habitus of (90) *Acontistoptera brasiliensis* Schmitz (not Nearctic) and (91) *Ecitomyia wheeleri* Brues; (92) head and thorax of *Chonocephalus* sp.; (93) left lateral view of head of *Trophodeinus pygmaeus* Borgmeier; habitus of (94) *Commoptera solenopsidis* Brues and (95) *Stenophorina petiolata* Borgmeier; (96) left lateral view of thorax of *Stenophorina petiolata*; (97) habitus of *Trophodeinus pygmaeus*; (98) wing of *Stenophorina petiolata*.

apex of R_{4+5}; apices of R_1 and R_{4+5} well removed from one another (Fig. 55). Mid and hind tibiae with two hair seams between which is a series of fine setae. (Male only; for female see couplet 57) .... ***Cataclinusa*** Schmitz, in part

1 sp., *pachycondylae* (Brues); Texas

Frons not noticeably narrowed and prolonged anteriorly; median furrow present. Apex of C not turned posteriorly toward apex of R_{4+5}; distance of apices of R_1 and R_{4+5} from each other variable. Mid and hind tibiae with one hair seam 53

53. Sc absent or not evident; R_1 and R_{4+5} approximated apically; bases of M_1 and M_2 approximated (Fig. 52). Frons usually longer than broad, with its sides nearly parallel (Fig. 23). Scutellum with two bristles and two small hairs. Tergite 6 of female abdomen mostly membranous .... ***Syneura*** Brues, in part

see couplet 37

Sc well-developed or clearly evident; R_1 and R_{4+5} not approximated apically; bases of M_1 and M_2 not approximated. Frons usually broader than long but sometimes quadrate or longer than broad. Scutellum with two, four, or rarely six bristles; when two present, two small hairs also present. Tergite 6 of female abdomen sclerotized, but with a membranous emargination at middle of anterior margin .... ***Megaselia*** Rondani, in part

see couplet 48

54. Head small, narrow. Thorax long, very narrow, flattened; lateral portions of mesonotum curving ventrally (Figs. 95, 96). R_{4+5} with a small incision at apex; posterior veins, thin, fading distally, not reaching margin of wing (Fig. 98). (Female only; male unknown)........ .... ***Stenophorina*** Borgmeier

1 sp., *petiolata* Borgmeier; Tennessee, New York

Head variable, but not strongly narrowed. Thorax normal in form, not long nor very narrow. Wing variable, but not with above combination of characters.................... 55

55. M_2 and CuA_1 strongly curved so as to form an hourglass-shaped cell between them (Fig. 56). Tergites of female abdomen reduced; segments 5 and 6 apparently fused together, with a semicircular plate-like gland cover .... ***Metopina*** Macquart

1 sp., *subarcuata* Borgmeier; widespread in U.S.A. and Quebec

M_2 and CuA_1 not strongly curved so as to form an hourglass-shaped cell between them. Abdomen of female variable, but not as above 56

56. Anterior margin of frons narrowed and prolonged between antennal grooves (Figs. 29, 31).... 57

Anterior margin of frons usually normal, but if pentagonal or slightly narrowed, then not prolonged between antennal grooves 58

57. Median furrow of frons present (Fig. 31). Anepisternum with a few hairs posterodorsally. Wing with well-developed microtrichia; humeral crossvein absent; apex of R_{4+5} with a small bubble-like swelling; basal one-quarter to one-third of M_1 obliterated (Fig. 57). (Male only; for female see couplet 69) .... ***Chonocephalus*** Wandolleck, in part

3 spp.; Ontario, eastern U.S.A.

Median furrow of frons absent (Fig. 29). Anepisternum bare. Wing without well-developed microtrichia; humeral crossvein present; bases of M_1 and M_2 approximated (Fig. 55). (Female only, but female of North American species unknown; for male see couplet 52).. ***Cataclinusa*** Schmitz, in part

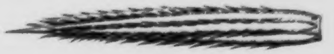
see couplet 52

58. Hind tibia with a hair seam and posterodorsal setae. Frons and vertex, in addition to supra-antennal bristles, with 14 major bristles arranged 2-4-4-4 (Fig. 32). R_{4+5} with a small angulate swelling near apex (Fig. 58). Female with a sclerotized ovipositor of varying shape (Fig. 85) .... ***Pseudacteon*** Coquillett

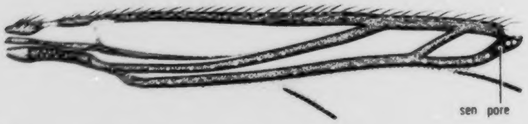
4 spp.; widespread in U.S.A. and British Columbia

Hind tibia without a hair seam, but sometimes with a series of posterodorsal setae or a single dorsal bristle. Frons and vertex with fewer than 14 major bristles, not arranged 2-4-4-4. R_{4+5} without an angulate swelling near apex. (Male only; female either unknown or with wings reduced or absent; if female apterous see couplet 21) 59

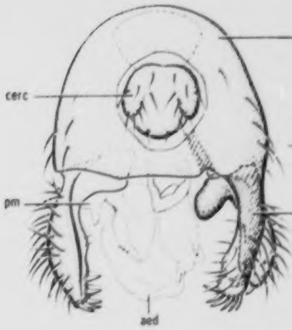
59. Bristles on frons and vertex arranged 2-4-4 or 2-4-6; only anterior fronto-orbital bristles absent. Palpus variable but usually not enlarged, although if somewhat elongated, then often with bristles. Terminalia not as below. (Male only) 60



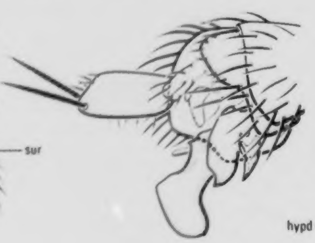
99 Chaetopleurophora sp. ♀



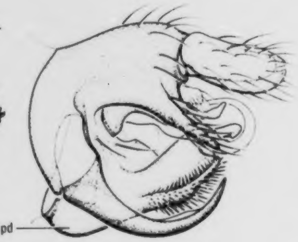
100 Gymnophora luteiventris ♀



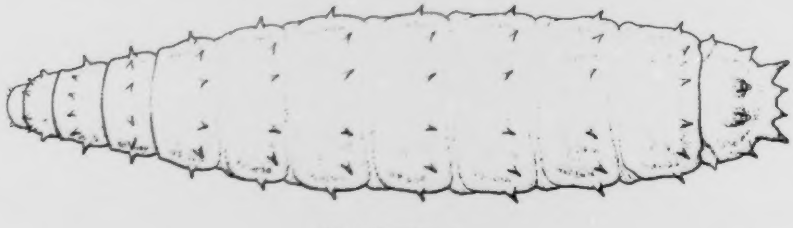
101 Conicera (Hypocerina) sp ♂



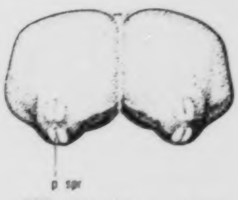
102 Cremersia spinicosta ♂



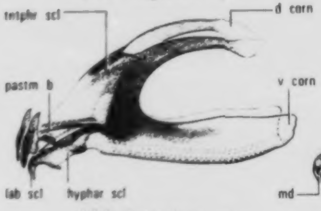
103 Bactropalpus furcatus ♂



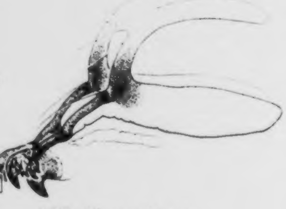
104 Megaselia sp.



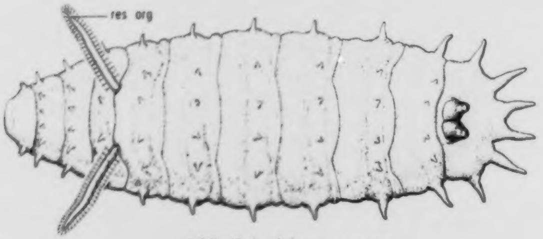
105 Dohrniphora cornuta



106 Spiniphora sp.



107 Megaselia sp.



108 Dohrniphora cornuta

Figs. 51.99–108. Bristle, portion of wing, male terminalia, larval features, and puparium: (99) bristle of *Chaetopleurophora* sp., showing feathering; (100) anterior veins of wing of *Gymnophora luteiventris* Schmitz, showing sensory pores, dorsal view; terminalia of (101) *Conicera* (*Hypocerina*) sp. in posterior view, (102) *Cremersia spinicosta* (Malloch) in left lateral view, and (103) *Bactropalpus furcatus* Borgmeier in right lateral view; (104) dorsal view of larva of *Megaselia* sp.; (105) posterior spiracles of larva of *Dohrniphora cornuta* (Bigot); cephalopharyngeal skeleton of larva of (106) *Spiniphora* sp. and (107) *Megaselia* sp.; (108) dorsal view of puparium of *Dohrniphora cornuta*.

Abbreviations: aed, aedeagus; cerc, cercus; d corn, dorsal cornu; epand, epandrium; hypd, hypandrium; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; pastm b, parastomal bar; pm, paramere; p spr, posterior spiracle; res org, respiratory organ; sen pore, sensory pore; sur, surstylus; tntphr scl, tentoropharyngeal sclerite; v corn, ventral cornu.

Bristles on frons and vertex arranged 0-0-6 or 0-2-6, with all bristles of anterior row absent; all other bristles short and fine. Palpus large, flattened, with short fine hairs (Fig. 33). Terminalia highly modified (Fig. 103). (Male only; female unknown) . . . ***Bactropalpus*** Borgmeier
4 spp.; southwestern and eastern U.S.A.

60. Frons with four supra-antennal bristles of nearly equal length; other bristles on frons and vertex arranged 2-4-6 61

Frons with two or four supra-antennal bristles of unequal length, with lower ones usually reduced; if these bristles nearly equal in length, then other bristles on frons and vertex arranged 2-4-4, but not 2-4-6 62

61. Frons without a median furrow (Fig. 34). Mid and hind tibiae with a row of fine posterodorsal setae; these setae sometimes tiny and difficult to see (Fig. 75). C less than half as long as wing (0.45 in only known North American species); Sc faint (Fig. 59). (Male only; for female see couplet 67 . . . . ***Acontistoptera*** Brues, in part
1 sp., *melanderi* Brues; Arizona, Texas, Kansas

Frons with a median furrow. Mid and hind tibiae without a row of fine posterodorsal setae. C half as long as wing or more (0.50 or greater); Sc distinct. (Male only; for female see couplet 69) . . . . ***Puliciphora*** Dahl, in part
7 spp.; widespread throughout North America

62. Mid and hind tibiae each with a single anterodorsal bristle at base (Fig. 73). (Male only; for female see couplet 67) . . . . ***Xanionotum*** Brues, in part
3 spp.; southern U.S.A.

Mid and hind tibiae without basal bristle 63

63. Supra-antennal bristles of unequal length. Hind tibia without a row of fine dorsal setae; hind trochanter with a pair of stout recurved spine-like bristles. (Male only; for female see couplet 66) . . . . ***Ecitomyia*** Brues, in part
1 sp., *wheeleri* Brues; Texas

Supra-antennal bristles about equal in length. Hind tibia with a row of fine dorsal setae. (Based on known males from South America; male of single North American species unknown; for female see couplet 65) . . . . ***Commoptera*** Brues, in part
1 sp., *solenopsidis* Brues; Texas

64. Wing present but reduced to rod-, spade-, or scale-like appendages (Figs. 60, 90, 91); halter and scutellum present or absent 65

Wing, halter, and scutellum absent 68

65. Ocelli present (Fig. 94). Wing rudiment spade- or scale-shaped, moderately broad, with membrane ending near apex of C (Fig. 60); halter and scutellum present. (Female only; for male see couplet 63) . . . . ***Commoptera*** Brues, in part
see couplet 63

Ocelli absent.[5] Wing rudiment rod-like, narrow; extent of membrane greatly reduced or entirely absent (Figs. 90, 91); halter and scutellum present or absent 66

66. Wing rudiment very small, without wing membrane, but covered dorsally with short hairs. Thorax not narrowed posteriorly; scutellum and halter absent (Fig. 91). (Female only; for male see couplet 63) . . . . ***Ecitomyia*** Brues, in part
see couplet 63

Wing rudiment longer, with at least some membrane present, and with bristles that are longer than wing rudiment itself. Thorax narrowed posteriorly; scutellum present; halter present or absent 67

67. Frons with six subequal supra-antennal bristles arranged in a nearly transverse row; anterior margin of frons with a series of short fine closely placed setae on each side or these in a single transverse row. Halter absent. Scutellum small, with two bristles. Abdomen covered with scattered fine hairs only (Fig. 90). Mid and hind tibiae without an anterodorsal bristle near base but each with a series of dorsal setae. (Female only; for male see couplet 61) . . . . ***Acontistoptera*** Brues, in part
see couplet 61

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[5] Ocelli are absent in the single North American species of *Ecitomyia* but are present in two Brazilian species of this genus.

Frons with four supra-antennal bristles. Halter present, but very small. Scutellum small, setose or bare. Abdominal tergites 2–5 each with one or two transverse rows of setae or bristles; setae or bristles few or numerous and closely placed, or sometimes rather stout and long (Fig. 86). Mid and hind tibiae each usually with a single anterodorsal bristle near base. (Female only; for male see couplet 62) .... ***Xanionotum*** Brues, in part

see couplet 62

68. Head and thorax longer than broad, slightly compressed laterally (Fig. 97). Proboscis stout and large (Fig. 93). Abdomen with seven free mostly membranous segments; apex of terminal abdominal segment semicircular, plate-like (Fig. 97). (Female only; male unknown) ... . ***Trophodeinus*** Borgmeier

2 spp.; Maryland, Michigan

Head and thorax at least as broad as long, not compressed laterally. Proboscis small. Abdomen with six free segments and five or six of these with tergal plates 69

69. Ocelli absent. Anterior margin of frons prolonged between antennal cavities. Thorax very short, emarginate on both anterior and posterior margins, and with short setae only (Fig. 92). Abdominal tergites 1–6 complete, with lateral margins variably produced ventrally. Sternite 6 with a sclerotized plate. (Female only; for male see couplet 57) .... ***Chonocephalus*** Wandolleck, in part

see couplet 57

Ocelli present. Frons normal, not prolonged between antennal cavities. Thorax reduced but not as much as above; at least hind margin straight or nearly so, bearing a series of fine but distinct bristles (Fig. 89). Abdominal tergites, especially 1 and 6, somewhat reduced; lateral margins of tergites not produced ventrally; tergite 5 with a gland opening at base; tergite 6 sometimes absent; sternite 6 membranous. (Female only; for male see couplet 61) ... . ***Puliciphora*** Dahl, in part

see couplet 61

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SYRPHIDAE

52

J. R. VOCKEROTH AND F. C. THOMPSON

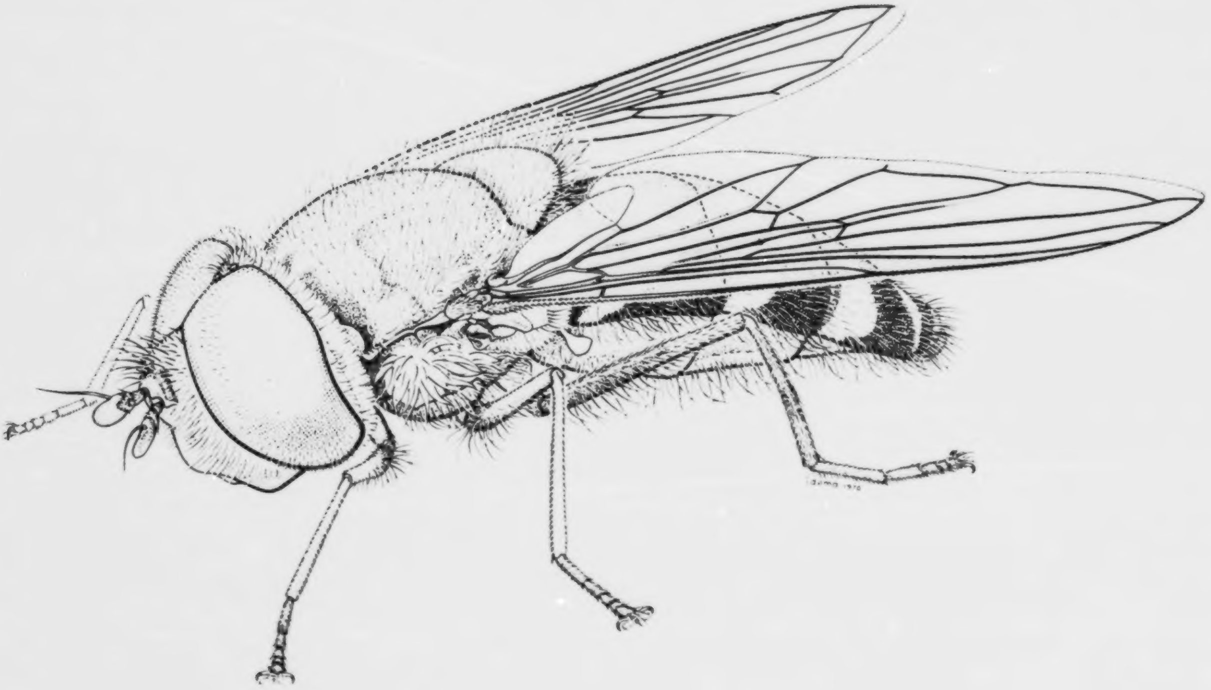
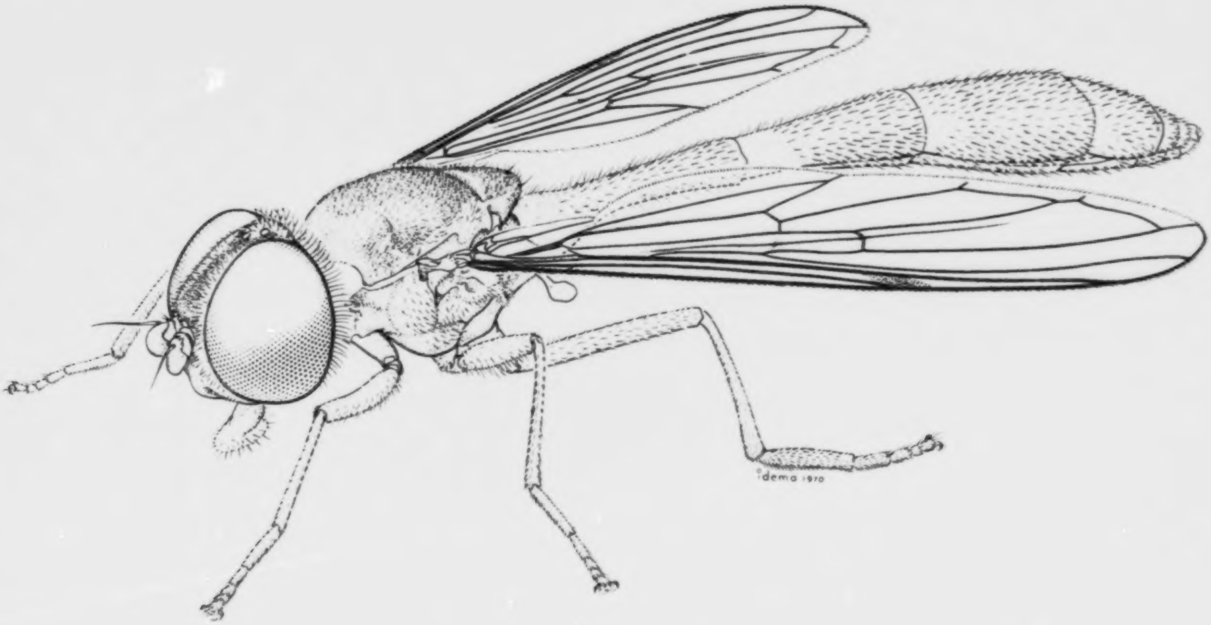


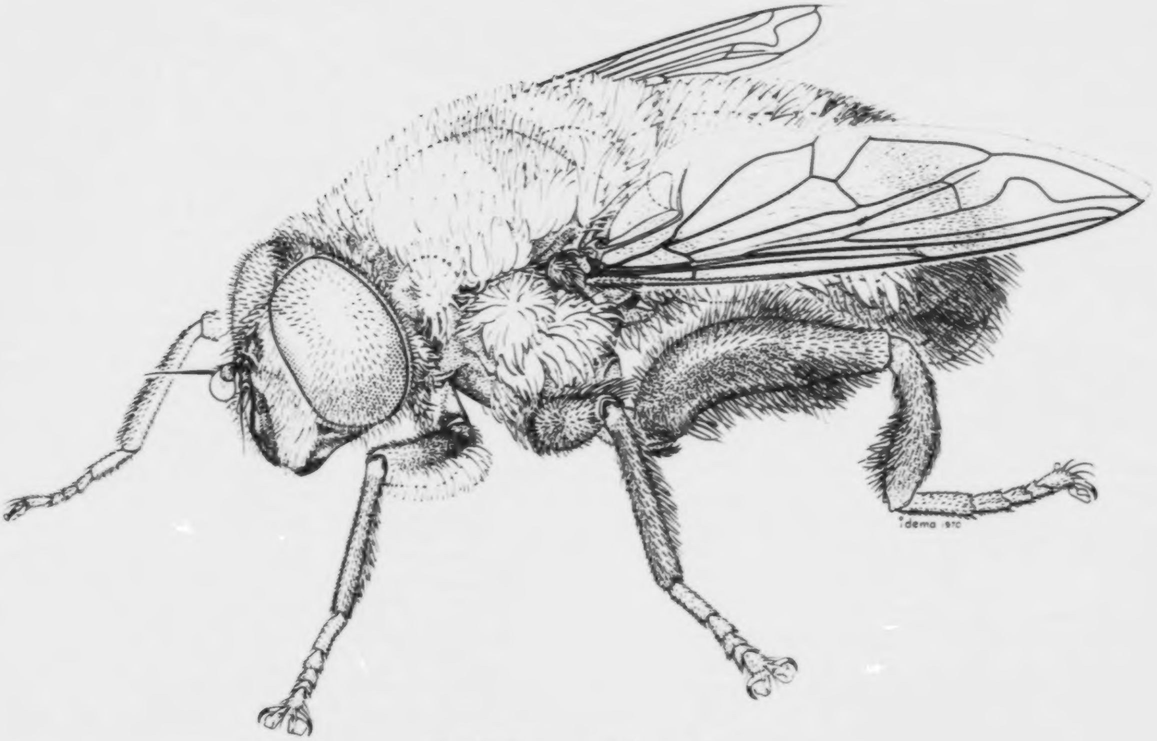
Fig. 52.1. Adult male of *Syrphus torvus* Osten Sacken.

Small to large, very slender to robust flies (Figs. 1-3), 4-25 mm long. Body usually black, very often with yellow or orange markings on head and thorax and particularly on abdomen, more rarely predominantly brown, yellow, metallic green, or blue, or with various combinations of these or other colors. Integument usually smooth but sometimes partly or totally punctate, sculptured, or rugose, usually nearly covered with dense short hairs, rarely with long hairs or nearly bare; some hairs sometimes flattened or scale-like and forming dense tomentum, or on thorax strong and bristle-like; both haired and bare portions shining, slightly to densely pruinose, or with very short dense pile. Many species excellent mimics of aculeate Hymenoptera.

Adult. Head: usually holoptic in male though sometimes very narrowly to broadly dichoptic, moderately to broadly dichoptic in female, without bristles. Some or all facets of upper part of eye sometimes enlarged in male; eye usually unicolorous, rarely with dark spots or bands, or with irregular markings, bare or with very short and sparse to long and dense hairs; these hairs rarely scale-like; three ocelli present. Facial profile varied, sometimes sexually dimorphic (Figs. 4-33); see Thompson (1972) for discussion. Mouthparts variable in length, usually correlated with length of subcranial cavity; taxonomic significance of variation unknown. Antenna sometimes borne on a short or long frontal prominence (Figs. 12, 13); scape and pedicel subcylindrical but varying greatly in length, with hairs or setae; first flagellomere varying greatly in shape, and often with a distinct sensory pit on lower part of inner surface; arista usually with two aristomeres but sometimes with three, usually dorsal but sometimes subapical or apical, usually longer than first flagellomere but very short in some Microdontinae and in some groups with apical arista, usually bare or with short pile, sometimes short to long plumose, rarely appearing strap-like because of very dense pilosity; antennal sockets confluent or separated. Lower facial margin usually with distinct median notch (Fig. 35), more rarely evenly rounded (Fig. 34). Frontogenal suture usually elongate, extending from anteroventral angle of eye for one-third or sometimes up to two-thirds distance to antennal base (Fig. 35), rarely reduced to an elongate anterior tentorial pit at anteroventral margin of eye (Fig. 34); face usually haired only laterad of frontogenal suture, sometimes entirely haired or with only median stripe bare.



2 Baccha elongata ♀



3 Mallota posticata ♂

Figs. 52.2–3. Adults: (2) female of *Baccha elongata* (Fabricius); (3) male of *Mallota posticata* (Fabricius).

Thorax: nearly uniform in structure but sometimes with modifications. Scutum sometimes flattened on posterior half; scutellum sometimes with apical rim, sometimes with rounded apical notch and a pair of short slender preapical processes (Microdontinae), sometimes produced as a conical triangle (*Lepidomyia* Loew), or with a discal depression or with lateral or median tubercles or both (some Volucellini); notopleuron sometimes strongly enlarged (*Ornidia* Lepeletier & Serville) or projecting posteriorly over wing base (*Nausigaster* Williston) (Fig. 74). Anepisternum sometimes uniformly convex, not divided into a flat anterior and a concave posterior portion (Fig. 74). Precoxal bridge absent; postcoxal bridge sometimes partly or completely developed (Figs. 79–81); metasternum variable in development, each half ranging from a slender anterior and submedian sclerotized strip through various intermediate forms to a large unexcavated sclerite (Figs. 70–73, 75, 76).

Distribution of thoracic hairs (and bristles, if present) varied, taxonomically important (Vockeroth 1969, Thompson 1972). Distinct bristles or spines sometimes present on anepisternum, notopleuron, postalar callus, prescutellar area of scutum, and scutellar margin; thorax otherwise with only fine hairs. Prothorax with postpronotum and other sclerites haired or bare. Scutum sometimes with transverse row of long erect hairs near anterior margin; scutellum bare below or with posteroventrally or ventrally directed hairs in one or more rows near posterior margin of ventral surface (ventral scutellar fringe) (Fig. 63). Anepisternum always with convex posterior portion haired, and with flattened anterior portion (if distinct) bare or with erect hairs (Fig. 65); katepisternum usually with distinct posterodorsal or ventral hair patches that are sometimes narrowly or broadly joined, rarely with one or both patches absent, sometimes with hairs also present anterodorsally or along anteroventral margin (Figs. 66–69). Anepimeron with anterior section always haired at least on upper half, with dorsal triangular section below wing base usually bare but sometimes densely haired (Fig. 64), and with posteroventral section usually bare but sometimes partly or entirely haired; katepimeron haired in all Syrphinae but haired or bare in other subfamilies; meron usually bare but sometimes with hairs situated in front of and below spiracle; laterotergite with only short dense pubescence, with long erect hairs only in some Old World Syrphinae. Metepisternum and metepimeron usually bare, but either sclerite sometimes with a few hairs; postcoxal bridge, if present, bare; metasternum haired or bare.

Wing (Figs. 40–60) with characteristic venation, with much variation in minor details but always with these main features: C ending at apex of R_{4+5}; an unattached longitudinal vein called the spurious vein present, running most of length of cells br and r_{4+5}, although this vein very faint in some exotic species; apex of M bent strongly forward near wing margin to end in R_{4+5} and forming apical crossvein; cell cu*p* closed near wing margin. Pterostigma usually present, extending to apex of R_1, sometimes shortened or represented only by crossvein sc extending from near apex of Sc to R_1. Branches of R and M sometimes with short stump veins; upper surface of Rs usually with several long fine bristles, rarely bare; veins other than C bare. Wing membrane usually hyaline but sometimes darkened or with discrete dark markings, sometimes entirely covered with microtrichia but often without microtrichia on part or all of one or both surfaces; bare areas usually near base of wing but sometimes apical part of wing, or rarely entire wing, without microtrichia. Wing shape nearly uniform but anal lobe and alula sometimes much reduced or absent, especially in forms with a petiolate abdomen. Calypteres well-developed; lower one sometimes with erect fine to coarse hairs on upper surface (Fig. 62), with or without long marginal fringe. Plumule short to long, rarely absent, with short to long fringe.

Legs (Figs. 82–92) usually slender and simple but sometimes (especially in male) with coxa, trochanter, femur, tibia, or tarsus modified; hind coxa or trochanter sometimes bearing a spur, spines, or a tubercle; femur sometimes swollen or distorted, often bearing anteroventral or posteroventral preapical spines or a preapical flange or spur; tibia sometimes arcuate, bearing an apical spur or otherwise modified; tarsus sometimes broadened and depressed or first tarsomere (especially on hindleg) sometimes strongly swollen; tarsal claws always curved and tapering to an acute apex except in male of Ethiopian species of *Ischiodon* Sack (Syrphinae).

Abdomen: extremely varied in shape; usually suboval, sometimes short and broad, more frequently elongate and petiolate (slender basally, broadened apically), rarely broadened basally and slender toward apex (Figs. 93–101). Margins of tergites usually curved uniformly downward laterally (Figs. 95, 96); in many Syrphinae tergites 2–5 or 3–5 with a submarginal longitudinal impression producing a marginated abdomen (Figs. 94, 97–100); in *Chrysotoxum* Meigen posterolateral angles of tergites often produced to give a serrated margin (Fig. 94). Abdominal spiracle 1 in Microdontinae, Merodontini, and Pipizini situated in membrane between tergite 1 and sternite 1, in other groups in a sclerotized area that is apparently an anteroventral extension of tergite 1; spiracles 2–7 of both sexes situated in membrane between corresponding tergites and sternites.

Male with tergite 5 visible in Syrphinae (Figs. 94–100), but in other subfamilies this tergite not visible externally (Fig. 101). Sternites 1–5 usually well-developed, sometimes very slender, rarely with tubercles, keels, or other modifications; sternite 1 unsclerotized only in some species of *Sphegina* Meigen (Fig. 80). Terminalia (Figs. 102, 103) rotated through 360°; segments 5 (or 6) to 8 rotated through 180°; segment 9 rotated through an additional 180°, so that sternite 8 lies immediately behind tergite 9 (epandrium); terminalia at same time flexed forward so that segment 9 normally lies in an asymmetric position below tergite 4 or 5 and surstyli and aedeagus are directed forward (Fig. 102). Sternite 8 usually smoothly rounded externally, rarely with processes. Tergite 9 (epandrium) usually a hollow curved shell, open ventrally; a pair of usually weak and compressed but sometimes highly modified cerci set in a posterodorsal notch that is rarely (in most *Sphaerophoria* Lepeletier & Serville and in some *Ocyptamus* Macquart) closed posteriorly, so that cerci are thereby surrounded by tergite 9. Pair of articulated surstyli of varied shape at posterolateral angles of tergite 9; base of each surstylus with an internal apodeme projecting anteriorly below tergite 9; these apodemes fused medially, articulated anteriorly with anterodorsal angle of sternite 9 (hypandrium), and apparently representing sternite 10; sternite 10 in *Toxomerus* Macquart (Fig. 102), some *Copestylum* Macquart, and some genera of Pipizini bearing a haired weakly to strongly sclerotized external process projecting posteriorly between surstyli. Terminalia of two markedly distinct types: in Microdontinae (Fig. 105) sternite 9 having infolded posterodorsal surface, and lacking articulated apical lobes; aedeagus elongate, swollen basally, unsegmented, tubular, without lateral or dorsal processes although often divided apically into two parallel tubes; aedeagal apodeme double or absent; ejaculatory apodeme small; sperm duct strongly sclerotized distally, with a swollen and spherical basal portion partly enclosed by base of aedeagus, and with an elongate apical portion completely enclosed by aedeagus; terminalia of most species of Microdontinae almost identical. In Syrphinae and Eristalinae (Fig. 104) sternite 9 lacking infolded posterodorsal surface and having an articulated or fused process at each posteroapical angle called the paramere or superior lobe; aedeagus rarely elongate, never in the form of a simple elongate tube, strongly protruding or almost entirely enclosed within sternite 9, one- or two-segmented and often with distal segment forming an inflated semimembranous sac, usually with lateral or dorsal processes, and frequently with very complex sclerotization; aedeagal apodeme always present and single; sperm duct slender and membranous, but having at its proximal end a sclerotized ejaculatory apodeme that varies from very small to extremely large; terminalia of Syrphinae and Eristalinae extremely varied, offering excellent taxonomic characters at specific to tribal levels at least.

Female with at least tergites and sternites 1–5 exposed; sternite 5 sometimes partly withdrawn under sternite 4. Tergites and sternites 6–8 usually telescoped within preceding sclerites and weakly sclerotized; sometimes sternite 6, 7, or even 8 exposed and moderately to strongly sclerotized. Ovipositor (Fig. 106) usually slightly depressed to subcylindrical, rarely somewhat aciculate, generally ignored by taxonomists but with distinct specific differences in at least some species of *Toxomerus*, *Ocyptamus*, and *Orthonevra* Macquart. Three spermathecae present, small, apparently of little taxonomic significance, but so far not well-investigated.

Egg. Nearly uniform in shape, elongate-ovoid, without apical or lateral processes. Surface sculpturing varied, providing important taxonomic characters in some groups. Paper by Chandler (1968) important, describing and illustrating eggs of many British Syrphinae and Pipizini.

Larva. Extremely varied in habitus (Figs. 107, 109, 111, 113, 115), structure, habitat, and feeding habits. Form sometimes maggot-like or slightly to strongly flattened; segments sometimes bearing dorsal or lateral single or branched processes, especially toward posterior end; integument smooth, variously ornamented, or spinose. In some Milesiini prothorax and mesothorax bearing strong sclerotized hooks. In the Microdontinae (Fig. 107) form slug-like, without obvious segmentation, with a marginal fringe of fine processes, and usually with a dorsal vestiture of fine erect spicules arranged in clusters or in a hexagonal pattern. In all genera a single circular series of sensillae borne on thoracic segments 1–3 and on abdominal segments 1–8, at most 12 on each segment, but often fused or reduced in number; each sensilla normally raised on a papilla and surrounded by one or several setae. Prolegs present on mesothorax and abdominal segments 1–6 of most Eristalinae (Fig. 111), but much reduced or absent in some Eristalinae and all Syrphinae (Fig. 113) and Microdontinae; several rows of crochets usually present on each proleg in Eristalinae, but crochets sometimes reduced or absent. Eversible tracheated anal papillae probably present in all larvae; differences in branching evident, probably offering significant taxonomic characters.

First instar larva metapneustic; prothoracic spiracles (Fig. 110) usually appearing in second instar, in Eristalini only in third instar, and in plant-piercing *Chrysogaster* Meigen and in Microdontinae not appearing at all. Third instar of all known larvae except that of *Toxomerus politus* (Say) with posterior spiracles borne on a common process; this process short and nonretractile in Microdontinae (Fig. 108), Syrphinae (Fig. 114), and many Eristalinae (Figs. 112, 116), moderately to very long and telescopic in some Eristalinae (Fig. 111), and modified into an aciculate process for piercing aquatic plants for air supply in some species of *Chrysogaster*. Three straight to convoluted slit-like apertures usually present in each spiracle, but numerous radial slits (some *Volucella* Geoffroy, *Temnostoma* Lepeletier & Serville) or many pore-like openings (Microdontinae, Fig. 108) sometimes present instead. Four pairs of branched hairs on margin of fused spiracular plates usually present, but these often unbranched or absent in Pipizini, Syrphinae, and Microdontinae.

Mouthparts varied in structure, particularly important taxonomically and phylogenetically. Most detailed accounts those of Hartley (1963, morphology) and Roberts (1970, morphology and function). Four types evident: saprophagous (most Eristalinae), phytophagous (*Cheilosia* Meigen, Merodontini), predacious (Syrphinae, Pipizini), and scavenging (*Volucella*, Microdontinae). Saprophagous types having a complex comb-like mandibular lobe supported by a very slender reduced mandibular sclerite and having a highly musculated and contractile chamber (cibarium) within main part of cephalopharyngeal skeleton; fringed longitudinal ridges on floor of cibarium together with mandibular comb providing an effective filter-feeding apparatus for larvae living in aquatic or semiaquatic medium. Phytophagous types having much stronger mandibles and sometimes, at least, reduced ventral cibarial ridges, as well as sometimes a grinding pharyngeal apparatus for reducing particle size of plant tissue; larvae of Merodontini and perhaps at least those *Cheilosia* spp. living in decaying fungi, probably feeding on bacteria or fungal spores rather than on tissues of apparent host plant. Predacious types having four piercing stylets formed from labrum, mandibles, and fused labial lobes; cibarium strongly musculated, but because of concentrated diet no ventral filtering ridges present. Scavenging types (e.g.

Volucella inhabiting nests of Hymenoptera) having structures similar to those of saprophagous Eristalinae but with cibarial pump and filtering ridges reduced; structures of Microdontinae differing from those of other scavengers, showing some similarities (thin flat mandibles with ventral serration, sclerotized and pointed labium, absence of cibarial ridges) to predacious type; this similarity, although almost certainly due to convergence, not surprising because although some of these larvae feeding on solid pellets ejected from pharyngeal pockets of ants, others almost certainly predacious on immature stages of their hosts.

Pupa. Pupation occurring within contracted and eventually hardened larval skin. Newly formed pupal spiracles in Microdontinae and most Eristalinae varying greatly in length, shape, and nature of pores and protruding through dorsum of abdominal segment 1, sometimes apparent beneath surface but very rarely breaking through in Syrphinae. Eclosion of adult occurring by forcing open two opercula; one formed from dorsal part of thoracic segments; other formed by dorsal part of first abdominal segment.

Biology and behavior. The adults are among the most abundant and conspicuous of Diptera. Most if not all species are able to hover motionless in flight or to move in various directions. How this habit is associated with mating and with other activities such as feeding or dispersal is not clear. Most species are diurnal and very active, and certain European species move in large numbers over very long distances. All Syrphinae and Eristalinae probably visit flowers and feed on pollen and nectar. They are therefore significant pollinators of many plants, but their role as such has been little studied. This exposed feeding situation may be mainly responsible for mimicry of aculeate Hymenoptera, and mimicry is more frequent and better developed in the Syrphidae than in any other family of Diptera. The Microdontinae are not known to visit flowers; they are rather weak fliers and do not seem to move far from the larval habitat. Nevertheless, many species of Microdontinae apparently mimic Hymenoptera.

The larvae have a wide variety of habitats and food. Larvae of Microdontinae are known to live only in ant nests. Larvae of Syrphinae are predacious primarily on Aphidoidea and other Homoptera, but some species are known to feed on immature Thysanoptera, Coleoptera, or Lepidoptera. Larvae of Pipizini feed on Aphidoidea. Both these groups are probably important in controlling homopterous pests of cultivated plants, but little definite evidence of this role is available, and introductions of exotic predacious species as biological control agents in various parts of the world have not achieved any noticeable success. The feeding habits of Eristalinae are particularly varied. *Cheilosia* larvae feed in fungi or vascular plants; *Volucella* larvae are scavengers in nests of colonial Hymenoptera; *Copestylum* larvae live in decaying plant material, especially Cactaceae; Merodontini larvae live in monocotyledonous bulbs and sometimes in other plants and, although they are probably secondary invaders, are considered of considerable economic importance; larvae of *Tropidia* Meigen, *Syritta* Lepeletier & Serville, and *Rhingia* Scopoli live in dung or similar decaying organic material; Eristalini and Sericomyiini larvae live in water with a high organic content; larvae of *Neoascia* Williston, *Chrysogaster*, and *Orthonevra* are aquatic, with apparently some specific preference for relatively clean or polluted water; several other tribes of Eristalinae have larvae associated with tree holes, ulcerated tree wounds, or rotting wood. Larvae of a few Eristalini and *Syritta* have been known to cause intestinal myiasis in man, but this occurrence is apparently rare.

Classification and distribution. The classification of the Syrphidae has recently undergone extensive rearrangement. We recognize three subfamilies. The generic classification of the Nearctic Microdontinae (couplets 51 and 52) is that of Thompson (1969). The arrangement of the Syrphinae (couplets 2–38) is based largely on the work of Vockeroth (1969); keys to most of the Nearctic species are in preparation by Vockeroth. The classification of the Eristalinae is based primarily on the work of Thompson (1972, 1975). As treated here, the Eristalinae includes Milesiinae plus Pipizini minus Microdontini of Wirth *et al.* (1965), and the Milesiinae of Thompson (1972). A revised catalog of the Nearctic Syrphidae is in preparation by Thompson. The only tribe whose subfamily placement is still uncertain is the Pipizini (couplets 54, 55). The larvae of the Pipizini are apparently all predacious, as are those of the Syrphinae, but the characters of the adults suggest that the group should be referred to the Eristalinae. A thorough study of the larval mouthparts might indicate whether they show synapomorphy with those of the Syrphinae or whether the predatory habit has developed independently in the Pipizini.

The family is nearly world wide in distribution. In the New World, species occur from the northern limits of land south to Tierra del Fuego and the Falkland Islands. In general, native species are absent only from Antarctica and remote oceanic islands, e.g. Hawaii and many subantarctic islands. However, many species have been transported by human agency so that Hawaii now has 16 resident species and Easter Island two.

Of the 14 tribes of Syrphinae and Eristalinae recognized by us, 13 are widespread, occurring in most major zoogeographical regions. However, the Toxomerini, with the single genus *Toxomerus*, is a New World group, with over 100 Neotropical species and with 17 species occurring north of Mexico.

The distribution of most genera, unlike that of most tribes, is markedly restricted. There are a few exceptions. *Microdon* Meigen, as currently recognized, is nearly world wide in distribution and very diverse in appearance; it may eventually be divided into several genera. All species of Cerioidini (couplets 42–44) mimic wasps; as a result, the genera recognized here, some of which are nearly world wide, may be artificial groups based on similarities resulting from mimetically induced convergence.

Most genera are markedly restricted to the Holarctic, the Neotropical, or the Palaeotropical region. Rarely is a genus well developed in two of these regions and even more rarely is a genus represented more than intrusively in all three regions.

About 180 genera of Syrphidae are recognized and about 6000 species have been described. Approximately 870 species in 88 genera are Nearctic (*Palumbia* Rondani is doubtfully Nearctic). Forty-nine of these genera are predominantly Holarctic in distribution. In a few cases these genera have a subgenus (as now defined) with its greatest development elsewhere. *Chalcosyrphus* (*Neplas* Porter) is almost entirely Neotropical and *Paragus* (*Pandasyopthalmus* Stuckenberg) is predominantly Palaeotropical. Few of these 49 Holarctic genera have very many species. *Cheilosia*, with 77 Nearctic species and even more Palaearctic species, is the largest. *Platycheirus* Lepeletier & Serville, as here delimited, is almost as large; it also has many Palaearctic species, as well as a number in the Andes and in New Zealand. Together, these 49 genera contain about 75% of the Nearctic species.

Only eight genera are restricted to the Nearctic region. *Hiatomyia* Shannon has 22 species (possibly some poorly known eastern Palaearctic species should be placed here). *Hadromyia* Williston has six species; the other six genera each have only one or two.

The most distinctive group of genera, in terms of probable place of origin (or perhaps of speciation after migration from their place of origin), are the 10 genera that are otherwise exclusively Neotropical. They have a total of 99 species north of Mexico but have together 1067 species south of the United States, with many more not yet described. Most of these 99 species do not occur north of the southern United States and only 11 are known from Canada. The largest of these genera, in the Nearctic, are *Copestylum*, *Toxomerus*, *Ocyptamus*, and *Palpada* Macquart.

Ten genera, apart from *Microdon* and the four genera of Cerioidini referred to above, have anomalous distributions, with usually only a few species in each of several zoogeographical regions. *Orthonevra* has 16 Nearctic species and probably as many Palaearctic species, but it has also seven or more Neotropical species and possibly several in the Afrotropical region. *Allograpta* Osten Sacken is primarily circumtropical (Vockeroth 1969); the five Nearctic species occur in the Neotropical region as well and are almost certainly Neotropical in origin. The other genera in this category, e.g. *Psilota* Meigen, *Rhingia*, and *Tropidia*, pose interesting geographical problems and are well worth further study.

Three genera, *Meliscaeva* Frey, *Milesia* Latreille, and *Melanostoma* Schiner, are predominantly Palaeotropical in distribution. The first two are almost entirely Oriental, and the third has many Oriental and Afrotropical species. The Nearctic species of *Milesia* are undoubtedly endemic. The single species of *Meliscaeva* and of *Melanostoma* are Holarctic but were probably not introduced by man.

The six Nearctic species of the genera *Eumerus* Meigen, *Merodon* Meigen, *Syritta*, and *Eristalinus* Rondani have undoubtedly been introduced by man from Europe.

The literature on taxonomy and biology of both the adult and larva is extensive. The adult description given here is based on the studies of the present authors. The information on the larvae is derived mainly from the work of Heiss (1938), Dixon (1960), Hartley (1961, 1963), Dušek and Láska (1967), and Roberts (1970). Wirth *et al.* (1965) give references to many of the important papers on the family. Other important references are Bhatia (1939, aphidophagous larvae), Hippa (1968, genera of Palaearctic Syrphini), Hippa (1978, genera of the *Xylota* Meigen group), Boyes *et al.* (1971, cytotaxonomy of the Syrphinae), Boyes *et al.* (1980, cytotaxonomy of the Eristalinae and Microdontinae), Goeldlin de Tiefenau (1974, taxonomy and biology of Syrphinae of Switzerland), Shatalkin (1975, suprageneric classification), and Maier and Waldbauer (1979, mate-seeking strategies).

Fossil Syrphidae, apparently referable to two tribes of Syrphinae and six of Eristalinae, are known from the Eocene, Oligocene, and Miocene. Hull gave an excellent review of the 72 named species in 1945, and later Hull (1949*a*) gave a tabular summary and named several new genera. Thirty-two species are known from Baltic amber (31 Eristalinae, one possible Syrphinae); the others are from sedimentary deposits from western North America and Europe. Forty-five species are assigned to recent genera; the others belong to extinct genera, which do not differ markedly from living Syrphidae. Because of many changes in classification and the use of many additional taxonomic characters since Hull's study, the available material should be critically reexamined.

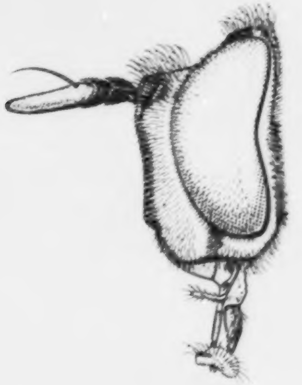
Key to genera

1. Postpronotum bare (Fig. 65). Head posteriorly strongly concave and closely appressed to thorax so that postpronota are partly or entirely hidden. Male abdomen with tergite 5 visible in dorsal view and varying in form from a subquadrate or subtriangular to a short transverse sclerite (Figs. 94–100) ....SYRPHINAE....2

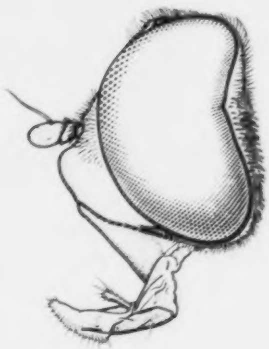
   Postpronotum with at least a few suberect or appressed hairs (Fig. 64). Head posteriorly less strongly concave so that postpronota are clearly exposed. Male abdomen with tergite 5 not visible in dorsal view (Fig. 101).........MICRODONTINAE, ERISTALINAE....39

2. Antenna elongate, sometimes longer than head; first flagellomere at least three times as long as wide; scape and pedicel often longer than wide (Fig. 4). Abdomen strongly convex dorsally, strongly marginated, usually with posterolateral angles of tergites projecting (Fig. 94) .... ***Chrysotoxum*** Meigen

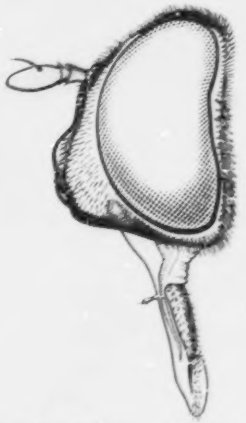
   about 7 spp.; widespread; Curran 1924, Shannon 1926*c*



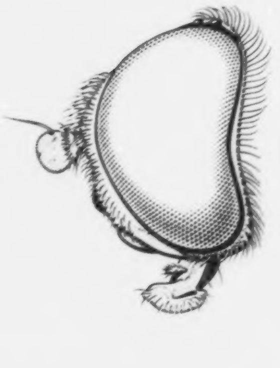
4 Chrysotoxum derivatum ♂



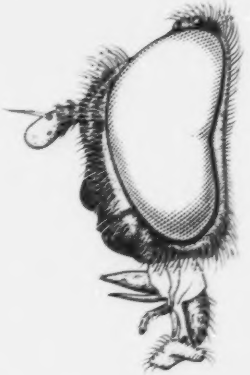
5 Toxomerus geminatus ♂



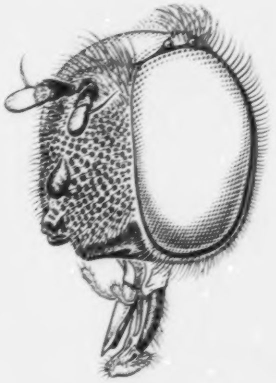
6 Pseudodoros clavatus ♂



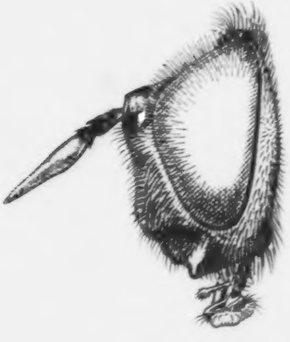
7 Baccha elongata ♂



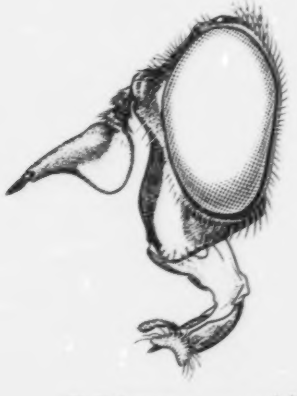
8 Melanostoma mellinum ♂



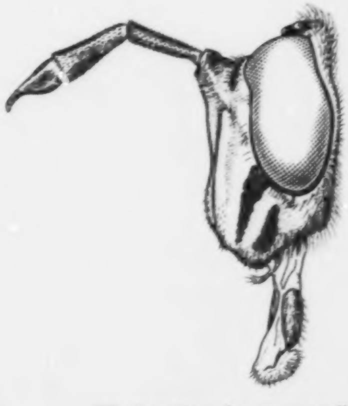
9 Platycheirus stegnus ♂



10 Callicera erratica ♂



11 Pelecocera pergandei ♂



12 Polybiomyia townsendi ♂

Figs. 52.4–12. Heads: (4) *Chrysotoxum derivatum* Walker; (5) *Toxomerus geminatus* (Say); (6) *Pseudodoros clavatus* (Fabricius); (7) *Baccha elongata* (Fabricius); (8) *Melanostoma mellinum* (Linnaeus); (9) *Platycheirus stegnus* (Say); (10) *Callicera erratica* (Walker); (11) *Pelecocera pergandei* (Williston); (12) *Polybiomyia townsendi* (Snow) (*continued*).

Antenna short, shorter than head; first flagellomere at most twice as long as wide; scape and pedicel not longer than wide (Figs. 5–9). Abdomen variable but without posterolateral angles of tergites projecting (Figs. 95–100) 3

3. Lower lobe of calypter with many long coarse yellow hairs above, especially on posteromedial portion (Fig. 62) .... **Syrphus** Fabricius

11 species; widespread; Vockeroth 1983

Lower lobe of calypter with only microscopic pile above or, rarely, with a few very fine pale scattered erect hairs 4

4. Posterior margin of eye with distinct triangular emargination that is at or above level of insertion of antennae (Fig. 5). Facial tubercle well-developed, beginning immediately below insertion of antennae and sometimes laterally compressed. Metasternum bare. Abdomen at least weakly marginated. Male with sclerotized, haired, very short to long triangular process arising from sternite 10 and projecting posteriorly between bases of surstyli (Fig. 102) .... **Toxomerus** Macquart

17 spp.; widespread; Hull 1943

Posterior margin of eye with emargination usually indistinct or shallow and rounded, but if distinct and subtriangular, situated below level of insertion of antennae (Figs. 6–8). Facial tubercle variable, sometimes indistinct or absent, not compressed. Metasternum bare or haired. Abdomen marginated or unmarginated. Male without sclerotized process projecting between bases of surstyli, with at most a weak bare semimembranous process in this position .. 5

5. Hind femur with distinct anteroventral and posteroventral spines on apical half. R_{4+5} slightly to strongly dipped into cell r_{4+5} (Fig. 45). Abdomen strongly petiolate (Fig. 95) .... **Salpingogaster** Schiner 6

Hind femur without spines. R_{4+5} usually straight or nearly so (as in Fig. 41). If R_{4+5} distinctly dipped into cell r_{4+5} (Figs. 40, 42–44), then abdomen not petiolate 7

6. R_{4+5} deeply dipped (Fig. 45). Tergite 1 produced laterally into a strong spur (Fig. 95). Upper occipital setae reduced to a single row .... **Salpingogaster** (**Salpingogaster** Schiner)

2 spp.; Texas and Florida; Curran 1932, 1941

R_{4+5} shallowly dipped. Tergite 1 not produced into a spur. Upper occipital setae in three or four rows .... **Salpingogaster** (**Eosalpingogaster** Hull)

1 sp., *nepenthe* (Hull); Florida

7. Anterior anepisternum with short to moderately long erect hairs, at least posterodorsally (Fig. 65) 8

Anterior anepisternum without hairs, with only microscopic pubescence 10

8. Hind coxa with tuft of hairs at posteromedial apical angle (Fig. 77). Eye bare or haired. Abdomen oval .... **Parasyrphus** Matsumura

10 spp.; widespread, including Arctic; Fluke 1935 (as part of *Epistrophe*)

Hind coxa without hairs at posteromedial apical angle. Eye bare. Abdomen oval, parallel-sided, or petiolate 9

9. Extreme posterior margin of wing with a series of minute closely spaced rounded black dots (Fig. 61). Metepisternum bare. Abdomen suboval to parallel-sided .... **Meliscaeva** Frey

1 sp., *cinctella* (Zetterstedt); widespread

Extreme posterior margin of wing without these dots. Metepisternum often with several fine hairs. Abdomen very variable, oval to strongly petiolate (as in Fig. 2) .... **Ocyptamus** Macquart

13 spp.; widespread; Hull 1949*b* (as part of *Baccha*)

10. Abdomen strongly petiolate (Fig. 2) 11

Abdomen parallel-sided to oval, never distinctly petiolate (Figs. 96–100) 14

11. Face produced rather strongly forward on lower half (Fig. 6) 12

Face not at all produced forward, either straight or with a very weak tubercle (Fig. 7) .. 13

12. Antennal sockets separated by about twice length of scape. Pleura mostly yellow; scutellum yellow .... **Allograpta** Osten Sacken, in part

5 spp.; widespread; Curran 1932, Fluke 1942

Antennal sockets separated by less than length of scape. Pleura black; scutellum yellow, with broad transverse black band .... ***Pseudodoros*** Becker

1 sp., *clavatus* (Fabricius); central U.S.A. southward

13. Face straight, without tubercle. Metepisternum with a row of fine subappressed hairs .... ***Leucopodella*** Hull

1 sp., *marmorata* (Bigot); southern Arizona

Face with low but distinct tubercle just above lower margin (Fig. 7). Metepisternum bare .... ***Baccha*** Fabricius

1 sp., *elongata* (Fabricius); widespread

14. Face and scutellum entirely black in background color. Abdomen unmarginated (as in Fig. 96). Metasternum bare. Eye bare 15

Face or scutellum or both at least partly yellow or yellow brown in background color, both never entirely black. Abdomen, metasternum, and eye variable 17

15. Metepisternum with several fine subappressed hairs; upper and lower katepisternal hair patches broadly separated posteriorly, joined anteriorly (Fig. 66). Hind coxa with tuft of hairs at posteromedial apical angle (as in Fig. 77) .... ***Xanthandrus*** Verrall

1 sp., *mexicanus* Curran; southern Texas

Metepisternum bare; katepisternal hair patches broadly separated throughout (as in Fig. 68). Hind coxa without hairs at posteromedial apical angle 16

16. Metasternum normal, with median portion broadly joined to lateral arms (Fig. 71). Face variable, almost straight with weak tubercle or moderately or strongly produced forward below, sometimes with pruinescence forming a punctate or rippled pattern (Fig. 9). Legs of male sometimes slender and unornamented, sometimes with fore tibia and tarsus broadened, or sometimes with femora or tibiae with bristles, hair tufts, or modified hairs .... ***Platycheirus*** Lepeletier & Serville

64 spp.; widespread, including Arctic; Curran 1927, 1930*b* (as *Platycheirus*, as part of *Melanostoma* and as *Pyrophaena* Schiner)

Metasternum greatly reduced, with deep posterior incision on each side so that median portion is narrowly joined to lateral arms (Fig. 70). Face not produced below, with small tubercle; facial pruinescence never punctate nor rippled (Fig. 8). Legs of male slender, without bristles, hair tufts, or modified hairs .... ***Melanostoma*** Shiner

1 sp., *mellinum* (Linnaeus)

17. Metapleuron with a tuft of fine hairs below spiracle; metasternum haired. R_{4+5} distinctly dipped into cell r_{4+5} (Fig. 40). Large species, with broad strongly marginated abdomen .... ***Didea*** Macquart

2 spp.; widespread; Vockeroth 1983

Metapleuron bare below spiracle; metasternum haired or bare. R_{4+5} straight or dipped. Size and shape variable 18

18. Scutum with a sharply defined clear yellow or whitish yellow lateral or sublateral stripe extending at least from postpronotum to transverse suture 19

Scutum with at most a poorly defined dull yellow pruinose lateral stripe 24

19. Abdomen with at least a weak margin on tergites 4 and 5, often with a strong margin on tergites 3–5 (Fig. 98) 20

Abdomen unmarginated (as in Fig. 96) 22

20. Upper part of katepisternum with sharply defined bright yellow spot 21

Katepisternum entirely dark or with at most a diffuse pruinose yellow area above .... ***Epistrophe*** (***Epistrophella*** Dušek & Láska), in part

1 sp., *emarginata* (Say); widespread

21. Abdomen strongly convex in cross section. Anepisternum black; scutellum unicolorous brown .... ***Doros*** Meigen

1 sp., *aequalis* Loew; widespread

Abdomen nearly flat. Anepisternum yellow posteriorly; scutellum bright yellow posteriorly .... ***Xanthogramma*** Schiner

1 sp., *flavipes* (Loew); eastern

22. Ventral scutellar fringe complete, well-developed, moderately dense (Fig. 63). Male terminalia small, inconspicuous; tergite 9 at most one-third as wide as abdomen 23

Ventral scutellar fringe absent or nearly so on at least median third, present but sparse laterally. Male terminalia extremely large, globose; tergite 9 as wide as abdomen .... ***Sphaerophoria*** Lepeletier & Serville
13 spp.; widespread; Knutson 1973

23. Metasternum bare .... ***Melangyna*** (***Meligramma*** Frey), in part
3 spp.; widespread; Vockeroth 1980

Metasternum haired (as in Fig. 76) .... ***Allograpta*** Osten Sacken, in part
see couplet 12

24. Wing with narrow but distinct brown band extending from anterior margin across crossvein r-m. Tergite 2 and base of tergite 3 yellow or gray; tergites otherwise black .... ***Leucozona*** (***Leucozona*** Schiner)
1 sp., *lucorum* (Linnaeus); widespread

Wing unmarked except for stigmal darkening. Tergites not colored as above 25

25. Metasternum bare 26

Metasternum with at least a few hairs (as in Fig. 76) 37

26. Eye distinctly haired 27

Eye bare or very nearly so (a few species of *Melangyna sens. str.* having very short and sparse eye hairs keying out in either alternative) 32

27. Tergite 1 well-developed, especially on disc where it is frequently half as long as tergite 2, and always extending well beyond scutellum, sublaterally about three-quarters as long as tergite 2 (Fig. 97); tergites minutely punctate. Length 7.5 mm or less .... ***Paragus*** Latreille.... 28

Tergite 1 greatly reduced, frequently almost linear on disc and practically covered by scutellum, sublaterally at most half as long as tergite 2 (Figs. 96, 98–100); tergites not punctate. Length 6.7 mm or more 29

28. Eye with hairs arranged in three more or less vertical bands of contrasting color. Scutellum black, with apex narrowly yellow or reddish .... ***Paragus*** (***Paragus*** Latreille)
several species, almost all undescribed; widespread

Eye with hairs of nearly uniform color, not forming bands of contrasting color. Scutellum entirely black .... ***Paragus*** (***Pandasyopthalmus*** Stuckenberg)
1 sp., *haemorrhous* Meigen; widespread

29. Wing membrane with at least apical third densely and uniformly trichose, without bare areas along veins. Male eye without well-defined area of enlarged facets above 30

Wing membrane with very sparse and scattered microtrichia and with extensive bare areas on apical third (Fig. 41). Male eye with well-defined area of enlarged facets above .... ***Scaeva*** Fabricius
1 sp., *pyrastri* (Linnaeus); western

30. Tergite 2 with large subquadrate gray or yellow spots that are much larger than pale markings on tergites 3 and 4 .... ***Leucozona*** (***Ischyrosyrphus*** Bigot)
2 spp.; widespread; Fluke 1935

Tergite 2 with oval or transverse yellow spots that are smaller than pale markings on tergites 3 and 4 (Figs. 96, 98–100) or tergite 2 entirely black ....

31. Abdomen unmarginated, slender and parallel-sided or narrowly oval (Fig. 96) .... ***Melangyna*** (***Melangyna*** Verrall), in part
7 spp.; widespread; Fluke 1935 (as part of *Epistrophe*)

Abdomen weakly but distinctly marginated (as in Fig. 98), oval.... ***Dasysyrphus*** Enderlein
7 spp.; widespread; Fluke 1933 (as *amalopis* group of *Metasyrphus*)

32. R_{4+5} at least moderately dipped into cell r_{4+5} (Figs. 42, 43) 33

R_{4+5} straight or nearly so (as in Fig. 41) 34

33. R_{4+5} moderately dipped (Fig. 42). Face with black median stripe...................... .... ***Eupeodes*** (***Lapposyrphus*** Dušek & Láska)
2 spp.; widespread; Fluke 1952

R_{4+5} very strongly dipped (Fig. 43). Face entirely yellow .... ***Dideomima*** Vockeroth
1 sp., *coquilletti* (Williston); southern Arizona

34. Abdomen with at least a faint trace of margin on tergite 3, 4, or 5 (Fig. 99). Face with at most an obscure dark stripe medially. Broader species, with oval or suboval abdomen 35

Abdomen entirely unmarginated (Fig. 96). Face often with clearly defined dark median stripe. More slender species, with nearly parallel-sided abdomen 36

35. Upper and lower katepisternal hair patches narrowly joined posteriorly (Fig. 67). Tergite 4 with entire yellow band (Fig. 99) .... ***Epistrophe*** (***Epistrophe*** Walker), in part
5 spp.; widespread; Vockeroth 1983

Upper and lower katepisternal hair patches broadly separated (Fig. 68). Tergite 4 with yellow band divided medially (Fig. 98) .... ***Epistrophe*** (***Epistrophella*** Dušek & Láska), in part
see couplet 20

36. Hind coxa with tuft of hairs at posteromedial apical angle (as in Fig. 77). Pale abdominal markings transverse; spots of tergites 2–4 always separated (Fig. 96). Face usually with black median stripe, rarely entirely yellow .... ***Melangyna*** (***Melangyna*** Verrall), in part
see couplet 31

Hind coxa without tuft of hairs at posteromedial apical angle. Pale abdominal markings oblique; spots sometimes confluent. Face entirely yellow .... ***Melangyna*** (***Meligramma*** Frey), in part
see couplet 23

37. R_{4+5} straight or nearly so (as in Fig. 41). Eye usually bare, rarely with distinct but very sparse hairs 38

R_{4+5} slightly but distinctly dipped into cell r_{4+5} (Fig. 44). Eye densely haired .... ***Eriozona*** (***Megasyrphus*** Dušek & Láska)
1 sp., *erraticus* (Linnaeus); widespread

38. Abdomen with strong distinct margin extending clearly from middle of tergite 2 to end of tergite 5 (Fig. 100). Upper and lower katepisternal hair patches very nearly confluent anteriorly, distinctly separated posteriorly (Fig. 69) .... ***Eupeodes*** (***Eupeodes*** Osten Sacken)
15 spp.; widespread, including Arctic; Fluke 1952 (as *Metasyrphus*)

Abdomen with very weak indistinct margin that begins on tergite 3 or 4 (Fig. 99). Upper and lower katepisternal hair patches broadly separated anteriorly, narrowly joined posteriorly (Fig. 67) .... ***Epistrophe*** (***Epistrophe*** Walker), in part
see couplet 35

39. Antenna with terminal stylus (Figs. 10–13) 40

Antenna with dorsal arista (Figs. 14–39) 45

40. Eye and face haired (Fig. 10). Crossvein r-m before middle of cell dm (as in Fig. 52). Ventral scutellar fringe present (as in Fig. 63) .... ***Callicera*** Panzer
4 spp.; eastern and southwestern; Curran 1935

Eye bare and face usually bare. If face haired, then crossvein r-m beyond middle of cell dm (as in Fig. 46). Ventral scutellar fringe absent 41

41. Crossvein r-m before middle of cell dm (as in Fig. 52). Antenna short; scape about as long as wide; first flagellomere large and longer than scape and pedicel combined (Fig. 11). Length 7 mm or less .... ***Pelecocera*** Meigen
1 sp., *pergandei* (Williston); eastern

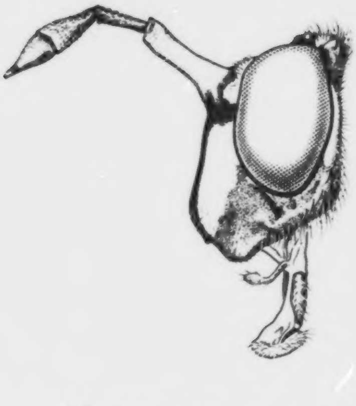
Crossvein r-m beyond middle of cell dm (Fig. 46). Antenna long; scape three to four times as long as wide; first flagellomere shorter than scape and pedicel combined (Figs. 12, 13). Length 8 mm or more 42

42. Frontal prominence absent or much shorter than scape (Fig. 12) 43

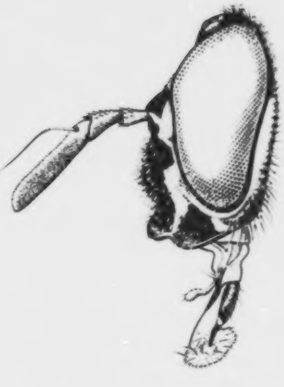
Frontal prominence at least as long as scape (Fig. 13) 44

43. Postcoxal bridge complete (Fig. 81) .... ***Polybiomyia*** Shannon
9 spp.; southwestern; Shannon 1925

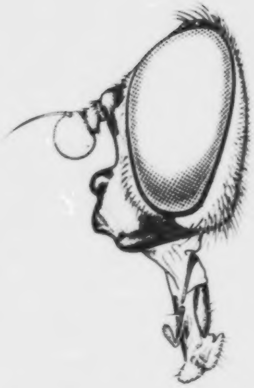
Postcoxal bridge incomplete, with a membranous area present above bases of hind coxae .. .. ***Sphiximorpha*** Rondani
8 spp.; widespread; Curran 1941 (as part of *Cerioides* Rondani)



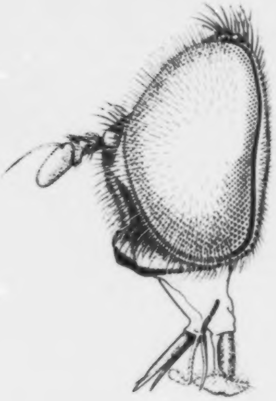
13 Ceriana abbreviata ♂



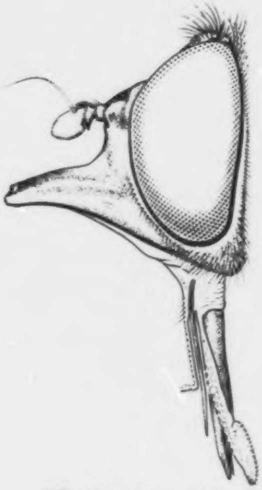
14 Lepidomyia micheneri ♂



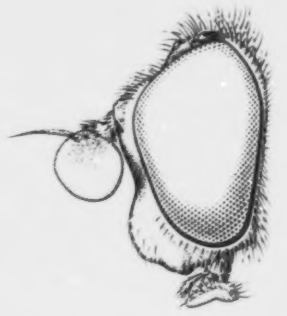
15 Myolepta varipes ♂



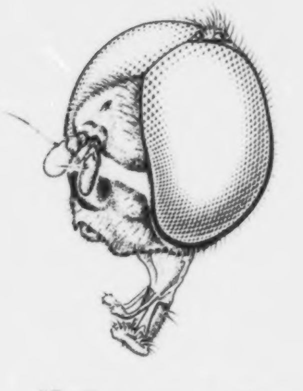
16 Psilota thatuna ♂



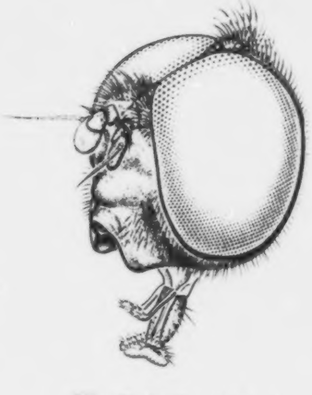
17 Rhingia nasica ♂



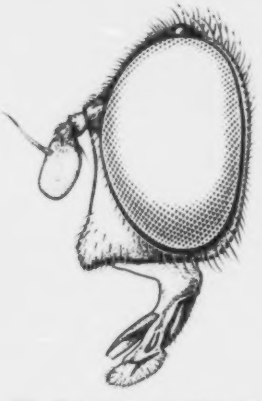
18 Chamaesyrphus willistonii ♂



19 Chrysogaster antitheus ♂

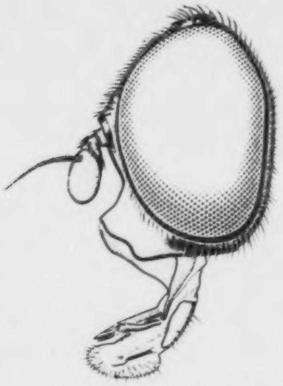


20 Cheilosia sialia ♂

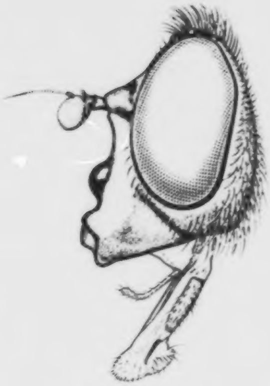


21 Neoascia metallica ♂

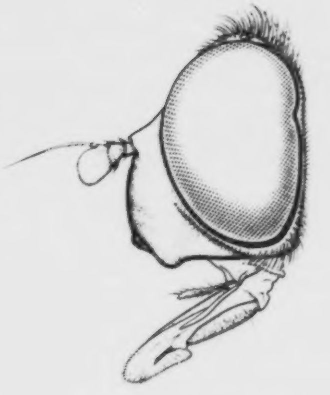
Figs. 52.13–21. Heads (*continued*): (13) *Ceriana abbreviata* (Loew); (14) *Lepidomyia micheneri* (Fluke); (15) *Myolepta varipes* Loew; (16) *Psilota thatuna* Shannon; (17) *Rhingia nasica* Say; (18) *Chamaesyrphus willistonii* (Snow); (19) *Chrysogaster antitheus* Walker; (20) *Cheilosia sialia* Shannon; (21) *Neoascia metallica* (Williston) (*continued*).



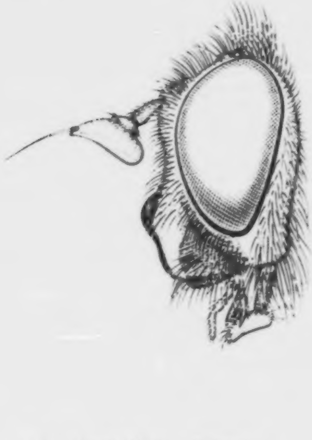
22 Sphegina (Sphegina) keeniana ♂



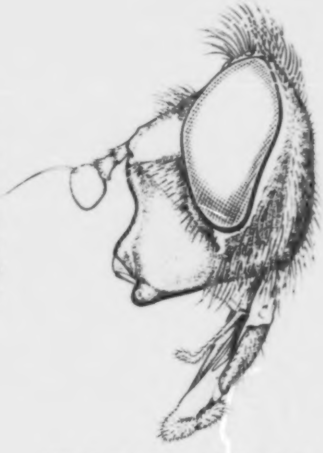
23 Cynorhinella bella ♂



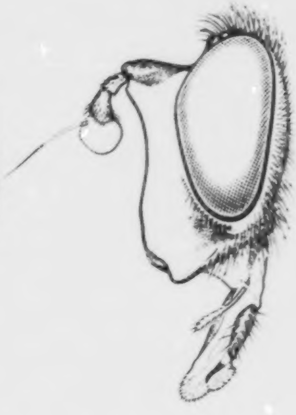
24 Tropidia quadrata ♂



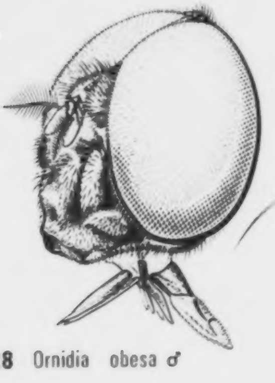
25 Merapioidus villosus ♂



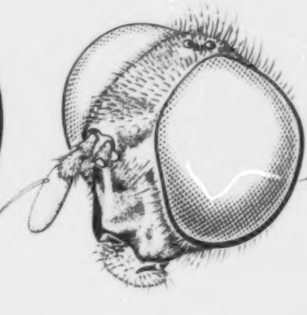
26 Brachypalpus (Crioprora) femoratus ♂



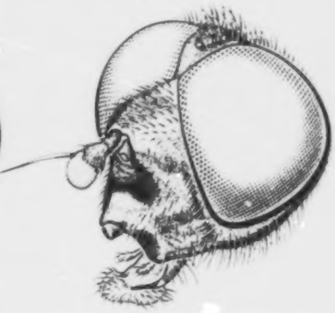
27 Somula decora ♂



28 Ornidia obesa ♂

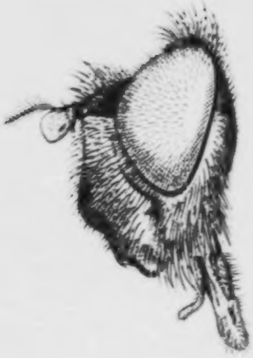


29 Chalcosyrphus (Neplas) pauxillus ♂

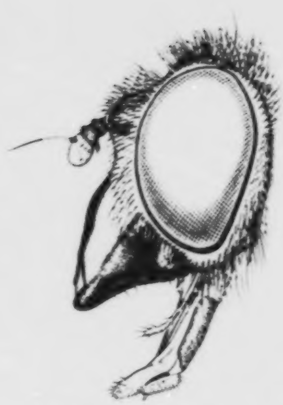


30 Chalcosyrphus (Chalcosyrphus) depressus ♂

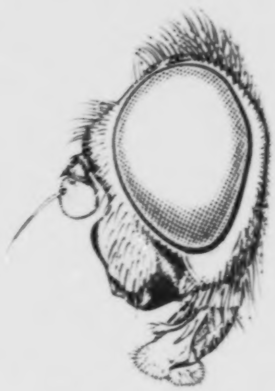
Figs. 52.22–30. Heads (*continued*): lateral views of (22) *Sphegina (Sphegina) keeniana* Williston, (23) *Cynorhinella bella* (Williston), (24) *Tropidia quadrata* (Say), (25) *Merapioidus villosus* Bigot, (26) *Brachypalpus (Crioprora) femoratus* (Williston), and (27) *Somula decora* Macquart; anterolateral views of (28) *Ornidia obesa* (Fabricius), (29) *Chalcosyrphus (Neplas) pauxillus* (Williston), and (30) *Chalcosyrphus (Chalcosyrphus) depressus* (Shannon) (*continued*).



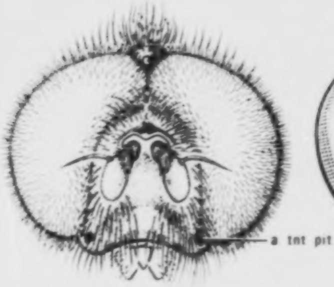
31 Pyritis kincaidii ♂



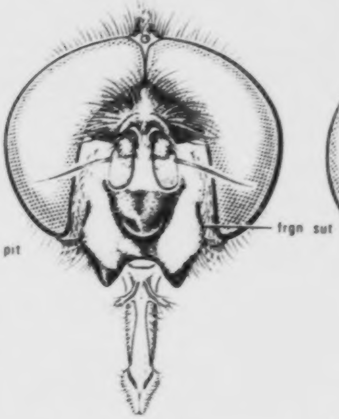
32 Lejops (Arctosyrphus) willingii ♂



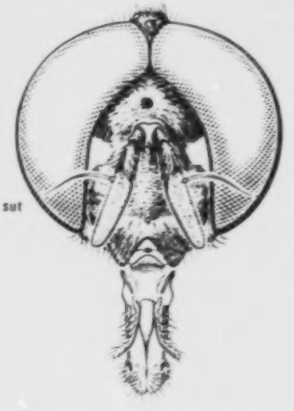
33 Lejops (Lunomyia) cooleyi ♂



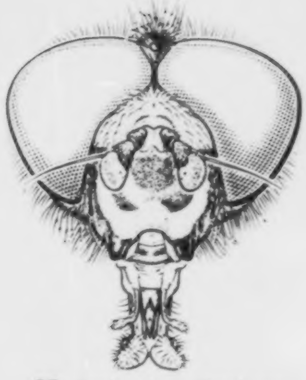
34 Pipiza quadrimaculata ♂



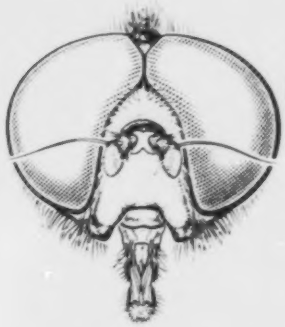
35 Cheilosia capillata ♂



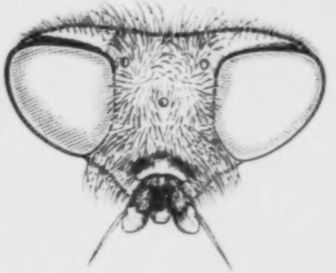
36 Orthonevra pulchella ♂



37 Brachypalpus (Brachypalpus) oarus ♂

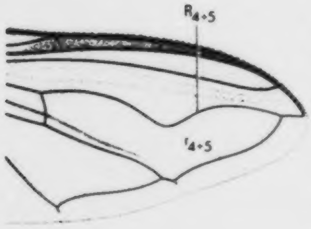


38 Xylota barbata ♂

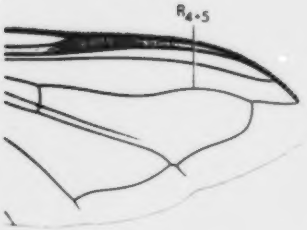


39 Lejops (Asemosyrphus) polygrammus ♂

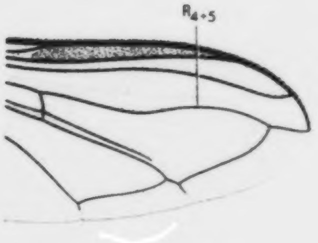
Figs. 52.31–39. Heads (*concluded*): lateral views of (31) *Pyritis kincaidii* (Coquillett), (32) *Lejops* (*Arctosyrphus*) *willingii* (Smith), and (33) *Lejops* (*Lunomyia*) *cooleyi* (Seamans); anterior views of (34) *Pipiza quadrimaculata* (Panzer), (35) *Cheilosia capillata* Loew, (36) *Orthonevra pulchella* (Williston), (37) *Brachypalpus* (*Brachypalpus*) *oarus* (Walker), and (38) *Xylota barbata* Loew; (39) dorsal view of *Lejops* (*Asemosyrphus*) *polygrammus* (Loew).
Abbreviations: a tnt pit, anterior tentorial pit; frgn sut, frontogenal suture.



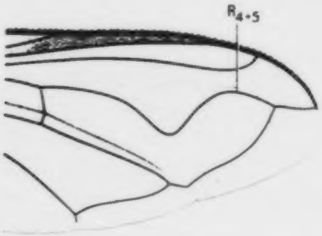
40 Didea fuscipes ♂



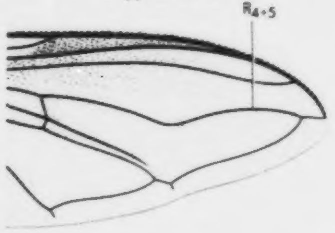
41 Scaeva pyrastri ♂



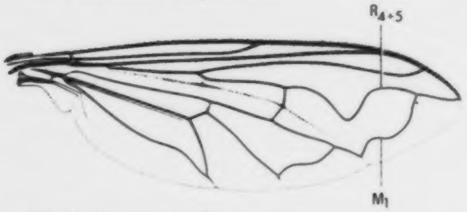
42 Eupeodes (Lapposyrphus) lapponicus ♂



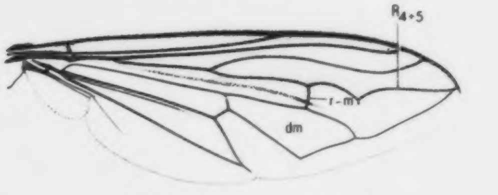
43 Dideomima coquilletti ♂



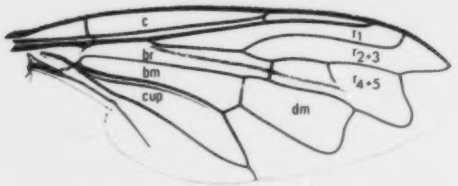
44 Eriozona erraticus ♂



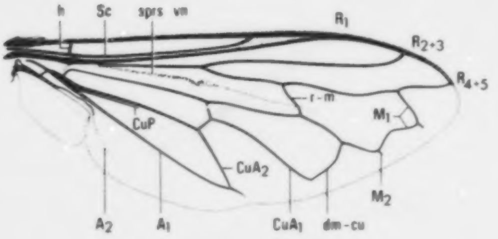
45 Salpingogaster (Salpingogaster) punctifrons ♂



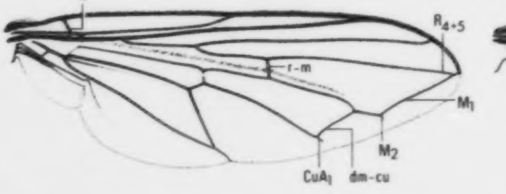
46 Ceriana abbreviata ♂


c
r1
br
r2+3
bm
r4+5
cup
dm

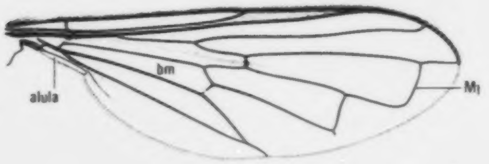
47 Microdon cothurnatus ♂


h
Sc
sprs vn
R1
R2+3
R4+5
r-m
M1
CuP
CuA2
M2
A2
A1
CuA1
dm-cu

48 Eumerus strigatus ♂


h
R4+5
r-m
M1
M2
CuA1
dm-cu

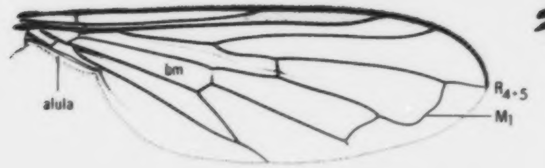
49 Cynorhinella longinasus ♂



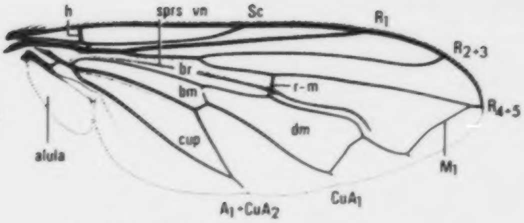
50 Neoascia distincta ♂

Figs. 52.40–50. Wings: outer half of wing, showing microtrichia, of (40) *Didea fuscipes* Loew, (41) *Scaeva pyrastri* (Linnaeus), (42) *Eupeodes (Lapposyrphus) lapponicus* (Zetterstedt), (43) *Dideomima coquilletti* (Williston), and (44) *Eriozona erraticus* (Linnaeus); complete wing of (45) *Salpingogaster (Salpingogaster) punctifrons* Curran, (46) *Ceriana abbreviata* (Loew), (47) *Microdon cothurnatus* Bigot, (48) *Eumerus strigatus* (Fallén), (49) *Cynorhinella longinasus* Shannon, and (50) *Neoascia distincta* Williston (*continued*).

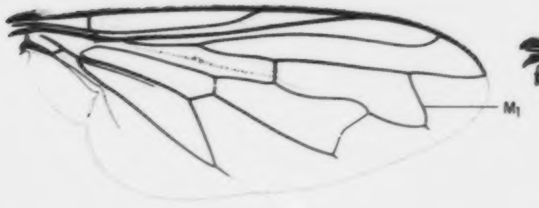
Abbreviations: sprs vn, spurious vein.


bm
alula
R4+5
M1

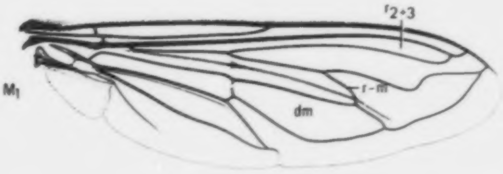
51 Sphegina (Sphegina) keeniana ♂


h
sprs vn
Sc
R1
R2+3
br
bm
r-m
R4+5
alula
cup
dm
M1
A1+CuA2
CuA1

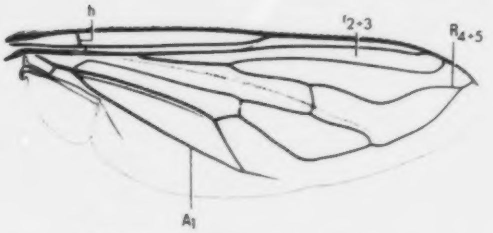
52 Brachyopa (Brachyopa) notata ♂



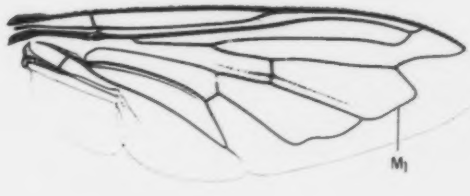
53 Orthonevra pulchella ♂



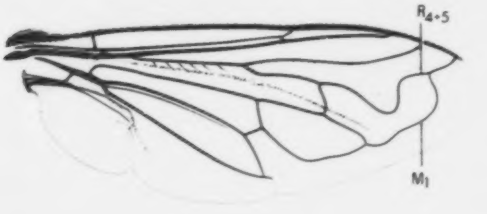
54 Milesia virginiensis ♂



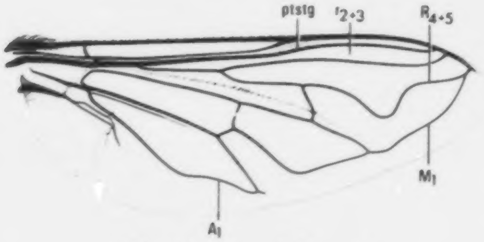
55 Teuchocnemis lituratus ♂



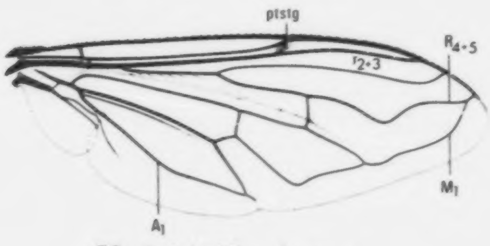
56 Volucella bombylans ♂



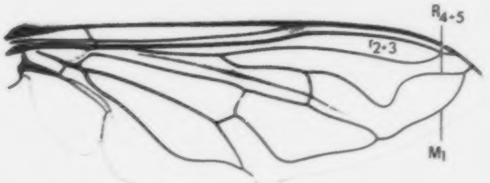
57 Merodon equestris ♂


ptstg
r2+3
R4+5
M1
A1

58 Helophilus latifrons ♂


ptstg
R4+5
r2+3
M1
A1

59 Parhelophilus laetus ♂



60 Eristalis (Eristalis) tenax ♂

Figs. 52.51–60. Wings (*concluded*): (51) *Sphegina (Sphegina) keeniana* Williston; (52) *Brachyopa (Brachyopa) notata* Osten Sacken; (53) *Orthonevra pulchella* (Williston); (54) *Milesia virginiensis* (Drury); (55) *Teuchocnemis lituratus* (Loew); (56) *Volucella bombylans* (Linnaeus); (57) *Merodon equestris* (Fabricius); (58) *Helophilus latifrons* Loew; (59) *Parhelophilus laetus* (Loew); (60) *Eristalis (Eristalis) tenax* (Linnaeus).
Abbreviations: ptstg, pterostigma; sprs vn, spurious vein.

44. R_{4+5} with a spur into cell r_{4+5} (Fig. 46). Abdomen not petiolate ...... ***Ceriana*** Rafinesque
5 spp.; widespread; Shannon 1925 (as *Tenthredomyia* Shannon)

R_{4+5} without spur. Abdomen petiolate .... ***Monoceromyia*** Shannon
1 sp., *floridensis* (Shannon); Florida

45. R_{4+5} straight or nearly so, not strongly dipped into cell r_{4+5} (Figs. 47–56) 46

R_{4+5} moderately to strongly dipped into cell r_{4+5} (Figs. 57–60)[1] 103

46. Arista bare or pubescent; if arista pubescent, then hairs never more than twice as long as basal diameter of arista (Figs. 14–27, 29–30, 34–38) 47

Arista plumose, with hairs at least three times as long as basal diameter of arista (Figs. 28, 31) 96

47. Fore and mid femora with short strong anteroventral and posteroventral spines near apex (Fig. 82) 48

Fore and mid femora without distinct spines 49

48. Antenna long; first flagellomere more than twice as long as wide; scape and pedicel elongate. Face tuberculate in both sexes (Fig. 14) .... ***Lepidomyia*** Loew
1 sp., *micheneri* (Fluke); southern Texas

Antenna short; first flagellomere less than twice as long as wide; scape and pedicel short. Face tuberculate in male (Fig. 15), concave in female .... ***Myolepta*** Newman
7 spp.; widespread; Fluke and Weems 1956

49. Eye haired or bare. If eye bare, crossvein r-m usually perpendicular, usually before middle of cell dm, never strongly oblique nor extending to outer third or more of cell dm (Figs. 49–53); if crossvein located above middle fifth of cell dm, then thorax with distinct bristles. Metasternum never strongly developed (Fig. 75) 50

Eye bare. Crossvein r-m always oblique, usually beyond middle of cell dm, frequently strongly oblique and extending to outer third of cell dm (Fig. 54); if crossvein located above middle fifth of cell dm (Fig. 55), then thorax without bristles. Metasternum often strongly developed (Fig. 76) 73

50. Antenna elongate, with scape and usually also first flagellomere more than 2.5 times as long as wide. Anterior anepisternum haired; postcoxal bridge narrow but complete (Fig. 79). R_{4+5} often with a spur into cell r_{4+5} (Fig. 47) 51

Antenna usually short; scape usually at most twice as long as wide; first flagellomere usually rounded or oval. If scape more than twice as long as wide, postmetacoxal bridge absent. Anterior anepisternum haired or bare; postcoxal bridge usually absent or incomplete, but if present broad (Fig. 80). R_{4+5} never with a spur into cell r_{4+5} 53

51. Katepisternum and posterior anepisternum bare; metasternum bare, reduced to a short transverse anterior sclerite with a narrow median posterior extension (Fig. 72). R_{4+5} without a spur. Abdomen petiolate .... ***Mixogaster*** Macquart
3 spp.; southern; Hull 1954

Katepisternum and posterior anepisternum with many hairs; metasternum haired, usually well-developed (Fig. 73). R_{4+5} with a spur into cell r_{4+5} (Fig. 47). Abdomen variable in shape 52

52. Katepimeron haired. Abdomen petiolate .... ***Rhopalosyrphus*** Giglio-Tos
1 sp., *carolae* Capelle; southwestern

Katepimeron bare. Abdomen parallel-sided or oval but not petiolate ..... ***Microdon*** Meigen
29 spp.; widespread; Thompson 1981

53. Facial margin evenly rounded, not notched anteromedially (Fig. 34); frontogenal suture reduced to a pit; eye and face densely haired. Ventral scutellar fringe present (as in Fig. 63) 54

Facial margin notched anteromedially (Fig. 35); frontogenal suture elongate, not forming a small round pit; eye and face haired or bare. Ventral scutellar fringe present or absent 56

54. Anterior anepisternum with long erect hairs (as in Fig. 65) ...... ***Trichopsomyia*** Williston
8 spp.; widespread; Curran 1921 (as *Pipizella* Rondani)

Anterior anepisternum bare 55

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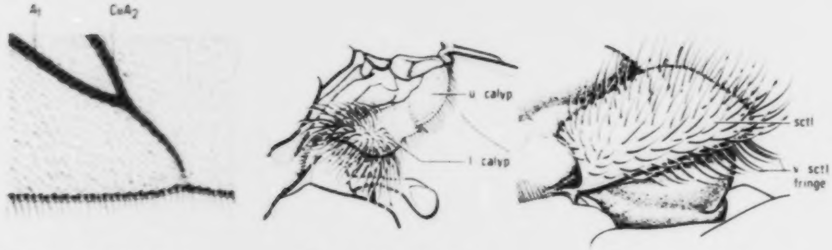
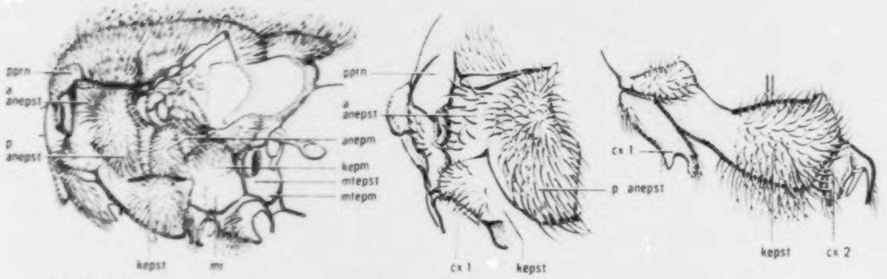
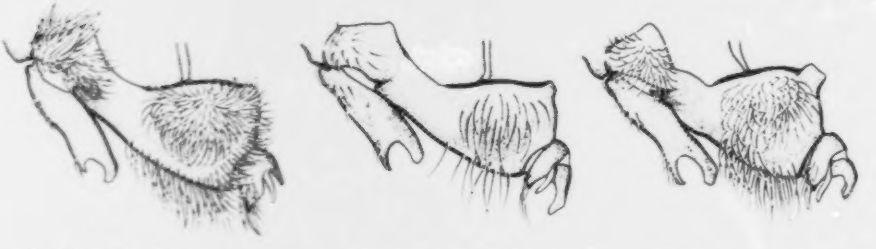
[1] The genera *Sericomyia* and *Arctophila* show considerable variation in the course of R_{4+5}; specimens key either way but eventually run to couplet 106, where the two genera are distinguished.



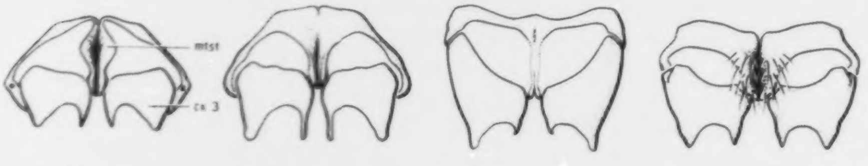
61 Meliscaeva cinctella ♂ **62** Syrphus ribesii ♂ **63** Allograpta obliqua ♂



64 Eristalinus aeneus ♂ **65** Meliscaeva cinctella ♂ **66** Xanthandrus mexicanus ♂



67 Epistrophe (Epistrophe) grossulariae ♂ **68** Epistrophe (Epistrophella) emarginata ♂ **69** Eupeodes (Eupeodes) americanus ♂



70 Melanostoma mellinum ♂ **71** Platycheirus quadratus ♂ **72** Mixogaster delongi ♂ **73** Microdon piperi ♂

Figs. 52.61–73. Details of wing and thorax: (61) *Meliscaeva cinctella* (Zetterstedt), posterior margin of wing; (62) *Syrphus ribesii* (Linnaeus), upper surface of lower calypter; (63) *Allograpta obliqua* (Say), posterolateral view of scutellum; (64) *Eristalinus aeneus* (Scopoli), lateral view of thorax; (65) *Meliscaeva cinctella*, lateral view of anterior part of thorax; katepisternum of (66) *Xanthandrus mexicanus* Curran, (67) *Epistrophe* (*Epistrophe*) *grossulariae* (Meigen), (68) *Epistrophe* (*Epistrophella*) *emarginata* (Say), and (69) *Eupeodes* (*Eupeodes*) *americanus* (Wiedemann); ventral views of metasternum of (70) *Melanostoma mellinum* (Linnaeus), (71) *Platycheirus quadratus* (Say), (72) *Mixogaster delongi* Johnson, and (73) *Microdon piperi* Knab.

Abbreviations: a anepst, anterior anepisternum; anepm, anepimeron; cx, coxa; kepm, katepimeron; kepst, katepisternum; l calyp, lower calypter; mr, meron; mtepm, metepimeron; mtepst, metepisternum; mtst, metasternum; p anepst, posterior anepisternum; pprn, postpronotum; sctl, scutellum; u calyp, upper calypter; v sctl fringe, ventral scutellar fringe.

55. Katepimeron bare. Male with distinct conically produced frontal prominence. Hind trochanter of male simple .... ***Pipiza*** Fallén

16 spp.; widespread; Curran 1921

Katepimeron haired at least anteriorly. Male with frontal prominence very short. Hind trochanter of male often with ventral spur .... ***Heringia*** Rondani

30 spp.; widespread; Curran 1921 (including *Cnemodon* Egger)

56. M_1 strongly biangulate, with an external spur; apical portion of M_1 forming on its outer side an acute angle with R_{4+5} (Fig. 48). Hind femur greatly enlarged, with anteroventral and posteroventral row of spines near apex. Eye haired .... ***Eumerus*** Meigen

3 spp.; widespread; Latta and Cole 1933

M_1 not strongly biangulate; apical portion usually forming a right or obtuse angle with R_{4+5} (Figs. 49–52); if apical portion of M_1 curved toward wing base (Fig. 53), then eye bare. Hind femur at most slightly enlarged 57

57. Anepisternum uniformly raised, not differentiated into a flattened anterior and a convex posterior portion; scutum with a lateral triangular extension above wing base (called the notopleural wing shield) (Fig. 74). Body densely punctate .... ***Nausigaster*** Williston

8 spp.; southwestern; Curran 1941

Anepisternum clearly differentiated into a flat anterior portion and a convex posterior portion (as in Fig. 65); notopleural wing shield absent. Body not punctate 58

58. Eye haired 59

Eye bare 61

59. Face without a tubercle but with lower margin projecting (Fig. 16). Anterior anepisternum haired (as in Fig. 65); scutellum with distinct marginal rim .... ***Psilota*** Meigen

3 spp.; western and southern U.S.A.

Face tuberculate, without projecting lower margin (Figs. 20, 35). Anterior anepisternum bare; scutellum without marginal rim, evenly convex apically 60

60. Crossvein r-m at or beyond middle of cell dm (as in Fig. 55). Antennal sockets confluent; face yellow with black median stripe. Legs yellow .... ***Ferdinandea*** Rondani

5 spp.; widespread; Hull 1942*a*

Crossvein r-m before middle of cell dm (as in Fig. 52). Antennal sockets separated; face black. Legs usually mostly black .... ***Cheilosia*** Meigen, in part

77 spp.; widespread; Hull and Fluke 1950 (in part, as *Cheilosia* and *Chilomyia* Shannon), Fluke and Hull 1946 (in part, as *Cartosyrphus* Bigot)

61. Ventral scutellar fringe present (as in Fig. 63) 62

Ventral scutellar fringe absent or nearly so 67

62. Face produced into a long porrect snout without tubercle (Fig. 17). C and R_{4+5} ending well beyond apex of wing .... ***Rhingia*** Scopoli

1 sp., *nasica* Say; widespread

Face usually not at all produced, but if moderately produced, directed downward as well as forward and bearing a tubercle (Fig. 23). C and R_{4+5} ending at or before apex of wing (Fig. 49) 63

63. Last section of R_{4+5} longer than crossvein h and usually longer than crossvein r-m 64

Last section of R_{4+5} shorter than crossvein h and at most half as long as crossvein r-m (Fig. 49) 66

64. Face yellow laterally, slightly concave above and convex below, usually haired ventromedially (Fig. 18). Arista bare or very nearly so; hairs shorter than basal diameter of arista. Male broadly dichoptic .... ***Chamaesyrphus*** Mik

3 spp.; southwestern; Curran 1923

Face entirely black or partly yellow, bare medially, either with a distinct tubercle clearly separated from oral margin (Figs. 19–20) or straight with lower margin projecting. If face partly yellow, aristal hairs distinctly longer than basal diameter of arista. Male holoptic 65

65. Face haired, with only a median stripe bare; hairs extending from just below level of antenna to subcranial margin; face of male tuberculate, sometimes weakly rugose laterally (Fig. 19); face of female straight with lower margin projecting; face and frons of female sometimes rugose. Scutellum without bristles .... ***Chrysogaster*** Meigen, in part

10 spp.; widespread; Fluke 1949

Face usually haired only between frontogenal suture and eye (Fig. 35); if hairs are present medial to frontogenal suture, they begin well below level of antenna and end well above subcranial margin (Fig. 20); face of both sexes with strong tubercle, smooth; frons smooth. Margin of scutellum sometimes with strong bristles .... ***Cheilosia*** Meigen, in part
see couplet 60

66. Last section of R_{4+5} less than half as long as crossvein h (Fig. 49). Hind femur with at least a weak spinose anteroventral preapical ridge (Fig. 87). Metasternum haired or bare. Eyes of male separated by, at most, width of anterior ocellus . . ***Cynorhinella*** Curran, in part
2 spp.; widespread; Shannon 1924

Last section of R_{4+5} subequal to crossvein h. Hind femur without an anteroventral preapical ridge. Metasternum bare. Eyes of male separated by about width of ocellar triangle ... . ***Lejota*** Rondani, in part
2 spp.; widespread; Fluke and Weems 1956

67. Abdomen petiolate. Alula narrower than width of cell bm (Figs. 50, 51). Postcoxal bridge entire (Fig. 80) or nearly so. Face concave or nearly straight, never tuberculate (Figs. 21, 22). Male broadly dichoptic 68

Abdomen parallel-sided or oval. Alula at least as wide as cell bm (Figs. 52, 53). Postcoxal bridge absent. Face variable, often tuberculate. Male holoptic or dichoptic 70

68. M_1 either perpendicular and forming a right angle with R_{4+5} or with its apical portion curved slightly toward wing base (Fig. 50). Face oblique, nearly straight (Fig. 21). Katepisternum usually haired .... ***Neoascia*** Williston
10 spp.; widespread; Curran 1925*a*

M_1 oblique, forming an acute angle with R_{4+5} (Fig. 51). Face convex (Fig. 22). Katepisternum bare .... ***Sphegina*** Meigen 69
25 spp.; widespread; Malloch 1922, Hull 1935, Coovert and Thompson 1977

69. Sternite 1 distinct, strongly sclerotized, subquadrate, haired .... ***Sphegina*** (***Sphegina*** Meigen)

Sternite 1 absent (Fig. 80) or present; if present, then much weaker than sternite 2, very slender, and bare .... ***Sphegina*** (***Asiosphegina*** Stackelberg)

70. Face and scutellum pale, orange to yellow; legs and abdomen extensively pale. Last section of R_{4+5} short, subequal to crossvein h (Fig. 52) .... ***Brachyopa*** (***Brachyopa*** Meigen), in part
13 spp.; widespread; Curran 1922

Face and scutellum black, usually with a metallic luster; legs and abdomen mostly black or dark metallic. Last section of R_{4+5} variable in length 71

71. Last section of R_{4+5} less than half as long as crossvein r-m. Male dichoptic. Face and frons of female smooth .... ***Lejota*** Rondani, in part
see couplet 66

Last section of R_{4+5} subequal to or longer than crossvein r-m (Fig. 53). Male holoptic. Face of both sexes and frons of female sometimes rugose (Fig. 36) 72

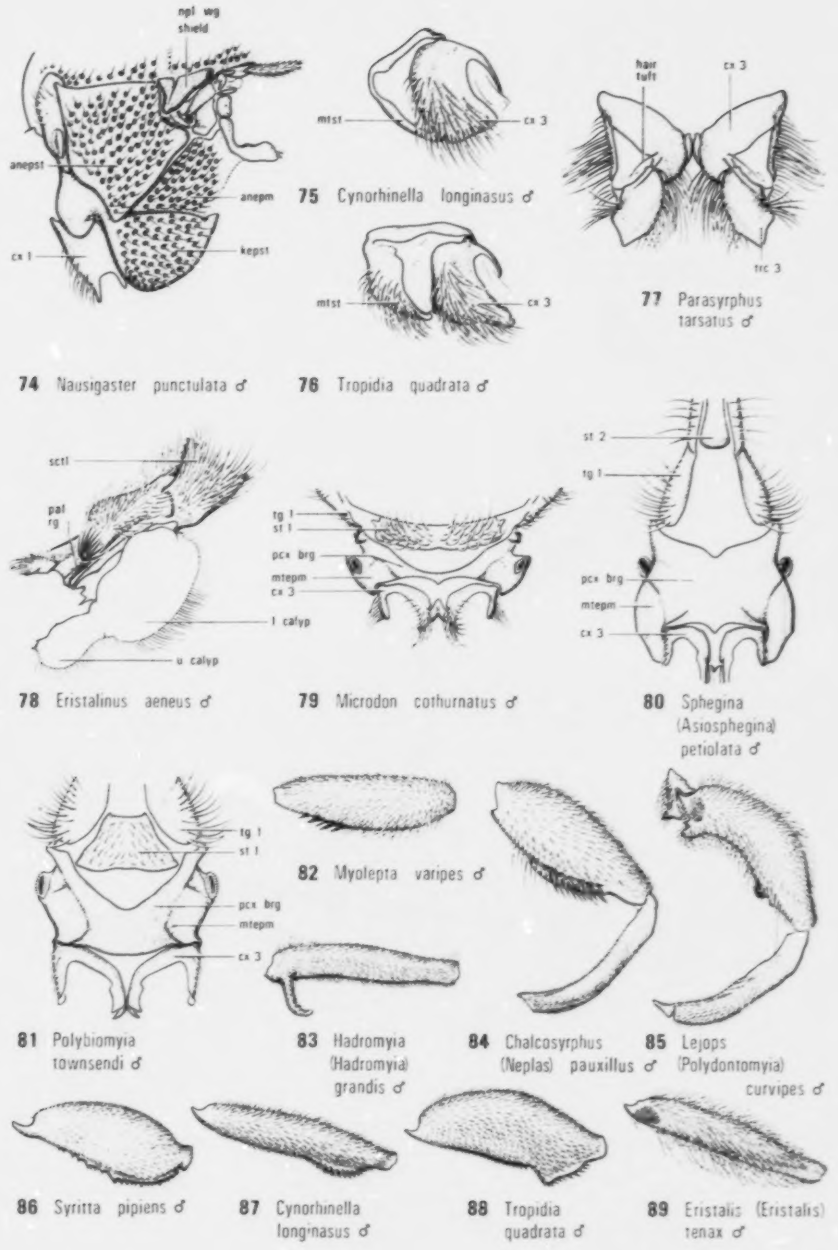
72. Sternite 1 shining, metallic. M_1 curved toward wing base (Fig. 53). First flagellomere usually at least twice as long as wide. Metasternum usually with a few short hairs .... ***Orthonevra*** Macquart
16 spp.; widespread; Shannon 1916, Sedman 1964 and 1966

Sternite 1 entirely pruinose. M_1 usually outwardly oblique, rarely curved very slightly toward wing base. First flagellomere at most 1.4 times as long as wide. Metasternum bare . . . . ***Chrysogaster*** Meigen, in part
see couplet 65

73. Cell r_{2+3} closed before wing margin (Fig. 54) .... ***Milesia*** Latreille
3 spp.; southern; Hull 1924

Cell r_{2+3} open to wing margin (Fig. 55) 74

74. Hind femur slender, with a slender unspined preapical anteroventral tooth-like process. Anterior anepisternum haired (as in Fig. 65). Large robust flies, mimicking wasps or hornets ... . ***Spilomyia*** Meigen
11 spp.; widespread; Curran 1951



74 Nausigaster punctulata ♂ **75** Cynorhinella longinasus ♂ **76** Tropidia quadrata ♂ **77** Parasyrphus tarsatus ♂

78 Eristalinus aeneus ♂ **79** Microdon cothurnatus ♂ **80** Sphegina (Asiosphegina) petiolata ♂

81 Polybiomyia townsendi ♂ **82** Myolepta varipes ♂ **83** Hadromyia (Hadromyia) grandis ♂ **84** Chalcosyrphus (Neplas) pauxillus ♂ **85** Lejops (Polydontomyia) curvipes ♂

86 Syritta pipiens ♂ **87** Cynorhinella longinasus ♂ **88** Tropidia quadrata ♂ **89** Eristalis (Eristalis) tenax ♂

Figs. 52.74–89. Details of thorax, abdomen, and legs: (74) *Nausigaster punctulata* Williston, dorsolateral view of anterior half of thorax; lateral views of metasternum and hind coxa of (75) *Cynorhinella longinasus* Shannon and (76) *Tropidia quadrata* (Say); (77) *Parasyrphus tarsatus* (Zetterstedt), posterior view of hind coxae and trochanters; (78) *Eristalinus aeneus* (Scopoli), postalar ridge; postcoxal bridge and base of abdomen of (79) *Microdon cothurnatus* Bigot, (80) *Sphegina* (*Asiosphegina*) *petiolata* Coquillett, and (81) *Polybiomyia townsendi* (Snow); (82) *Myolepta varipes* Loew, anteroventral view of fore femur; (83) *Hadromyia* (*Hadromyia*) *grandis* Williston, anterior view of mid femur; anterior views of hind femur and tibia of (84) *Chalcosyrphus* (*Neplas*) *pauxillus* (Williston) and (85) *Lejops* (*Polydontomyia*) *curvipes* (Wiedemann); anterior views of hind femur of (86) *Syritta pipiens* (Linnaeus), (87) *Cynorhinella longinasus*, (88) *Tropidia quadrata*, and (89) *Eristalis* (*Eristalis*) *tenax* (Linnaeus).

Abbreviations: anepm, anepimeron; anepst, anepisternum; cx, coxa; kepst, katepisternum; l calyp, lower calypter; mtepm, metepimeron; mtst, metasternum; npl wg shield, notopleural wing shield; pal rg, postalar ridge; pcx brg, postcoxal bridge; sctl, scutellum; st, sternite; tg, tergite; trc, trochanter; u calyp, upper calypter.

Hind femur not as above. If hind femur with a preapical anteroventral process, then femur swollen (Figs. 86–88) and anterior anepisternum bare. General appearance variable 75

75. Katepisternum continuously haired along posterior margin; anterior anepisternum haired or bare. Gena and lower part of face haired. Body with bright yellow pruinose markings; flies mimicking wasps . . . . **Temnostoma** Lepeletier & Serville

10 spp.; widespread; Curran 1939*b*, Shannon 1939

Katepisternum with separate dorsal and ventral hair patches; anterior anepisternum bare. Gena and lower part of face usually bare. If face haired, body entirely black. Body variable in appearance 76

76. Metasternum haired; hairs as long as or longer than those of hind coxa (Fig. 76) 77

Metasternum without hairs, with only very short pubescence 86

77. Wing membrane with microtrichia almost absent on basal two-thirds, very sparse and scattered on apical third. Metepisternum with a patch of fine hairs. Hind femur greatly enlarged, with an anteroventral spinose ridge on apical third (Fig. 86) . . . . **Syritta** Lepeletier & Serville

1 sp., *pipiens* (Linnaeus); widespread

Wing membrane entirely trichose or with moderate bare areas on approximately the basal third, densely and uniformly trichose on apical third. Metepisternum haired or bare. Hind femur variable 78

78. Hind femur with an apicoventral triangular plate or spinose ridge (Figs. 87, 88) 79

Hind femur without apicoventral process 80

79. Crossvein dm-cu and last section of M meeting at an obtuse angle, not continuous; at least a trace of M_2 and of CuA_1 beyond crossvein dm-cu present (Fig. 49). Metasternum small (Fig. 75). Face produced anteroventrally, extending about half its length below eye, not carinate, with a small tubercle; gena broad (Fig. 23) . . . . **Cynorhinella** Curran, in part

see couplet 66

Crossvein dm-cu and apical crossvein nearly continuous, without external spurs (as in Fig. 55). Metasternum very large (Fig. 76). Face not produced below, extending less than one-quarter its length below eye, carinate on at least lower half, without tubercle; gena narrow (Fig. 24) . . . . **Tropidia** Meigen

8 spp.; widespread; Shannon 1926*b*

80. Face concave, sometimes subcarinate, not tuberculate; gena narrow (Figs. 29–30). Body with short and sparse hairs, without bright yellow pruinose markings 81

Face produced downward, usually tuberculate; gena broad (Fig. 25). Body either with long hairs or with bright yellow pruinose markings 84

81. Face yellow in background color. Apical section of A_1 long, straight, not reaching wing margin (Fig. 55). Ventral scutellar fringe absent. Hind tibia of male with strong ventral spur (Fig. 90) . . . . **Teuchocnemis** Osten Sacken, in part

2 spp.; eastern; Williston 1887

Face mostly black in background color. Apical section of A_1 shorter, curved, reaching wing margin. Ventral scutellar fringe present (as in Fig. 63). Hind tibia of male without spur . . . . **Chalcosyrphus** Curran 82

82. Face subcarinate (Fig. 29). Hind femur greatly swollen and with ventromedial carina; hind tibia strongly arcuate (Fig. 84). Laterotergite carinate . . . . **Chalcosyrphus** (**Neplas** Porter)

1 sp., *pauxillus* (Williston); southern Arizona

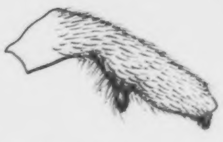
Face rounded medially, not subcarinate (Fig. 30). Hind femur less strongly swollen and without ventromedial carina; hind tibia not strongly arcuate. Laterotergite rounded, not carinate 83

83. Face haired below almost to midline (Fig. 30). Crossvein r-m situated before middle of cell dm. Scutum flattened in front of scutellum. Male narrowly dichoptic. Hind trochanter of male with ventral tubercle . . . . **Chalcosyrphus** (**Chalcosyrphus** Curran)

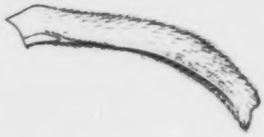
1 sp., *depressus* (Shannon); western

Face haired only laterally. Crossvein r-m situated at or beyond middle of cell dm. Scutum not flattened posteriorly. Male holoptic. Hind trochanter of male without tubercle . . . . **Chalcosyrphus** (**Xylotomima** Shannon)

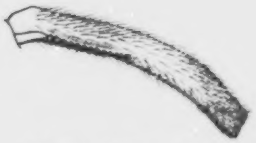
25 spp.; widespread; Shannon 1926*b* (as *Xylotomima* and *Xylotodes* Shannon), Curran 1941 (as part of *Heliophilus* Meigen)



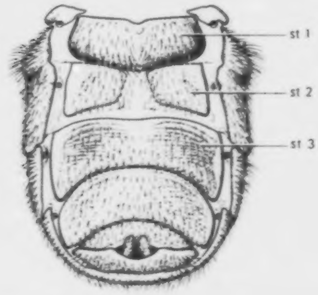
90 Teuchocnemis lituratus ♂



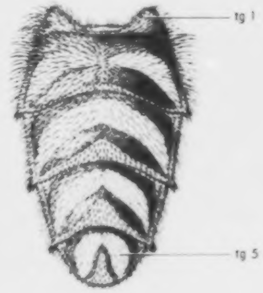
91 Lejops (Anasimyia) bilinearis ♂



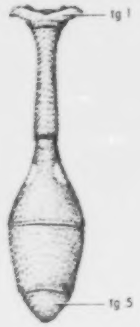
92 Parhelophilus laetus ♂



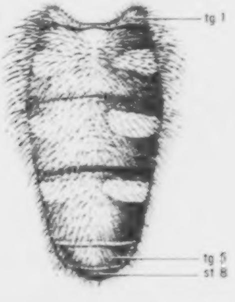
93 Lejops (Polydontomyia) curvipes ♀



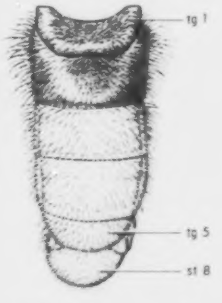
94 Chrysotoxum integre ♂



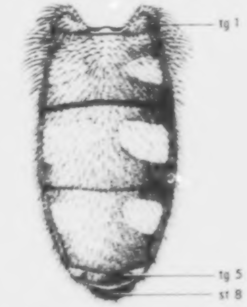
95 Salpingogaster (Salpingogaster) punctifrons ♂



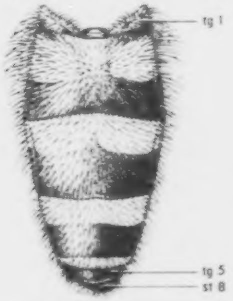
96 Melangyna (Melangyna) lasiophthalma ♂



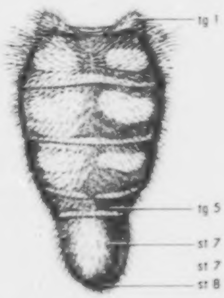
97 Paragus (Pandasyopthalmus) haemorrhous ♂



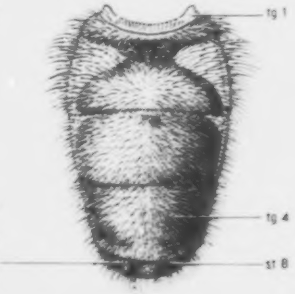
98 Epistrophe (Epistrophella) emarginata ♂



99 Epistrophe (Epistrophe) grossulariae ♂



100 Eupeodes (Eupeodes) volucris ♂



101 Blera badia ♂

Figs. 52.90–101. Legs and abdomens: (90) *Teuchocnemis lituratus* (Loew), anterior view of hind tibia; anteroventral views of hind tibia of (91) *Lejops (Anasimyia) bilinearis* (Williston) and (92) *Parhelophilus laetus* (Loew); (93) *Lejops (Polydontomyia) curvipes* (Wiedemann), ventrolateral view of abdomen; dorsal views of abdomen of (94) *Chrysotoxum integre* Williston, (95) *Salpingogaster (Salpingogaster) punctifrons* Curran, (96) *Melangyna (Melangyna) lasiophthalma* (Zetterstedt), (97) *Paragus (Pandasyopthalmus) haemorrhous* Meigen, (98) *Epistrophe (Epistrophella) emarginata* (Say), (99) *Epistrophe (Epistrophe) grossulariae* (Meigen), (100) *Eupeodes (Eupeodes) volucris* Osten Sacken, and (101) *Blera badia* (Walker).

Abbreviations: st, sternite; tg, tergite.

84. Arista inserted at apex of conically produced first flagellomere (Fig. 25) .... **Merapioidus** Bigot
1 sp., *villosus* Bigot; eastern

Arista dorsal 85

85. Thorax and abdomen with distinct yellow pruinose markings. Body with short and sparse hairs; flies mimicking wasps .... **Sphecomyia** Latreille
8 spp.; widespread; Weismann 1965, 1966

Thorax and abdomen without yellow pruinose markings. Body with long hairs; flies mimicking bumblebees .... **Criorhina** Meigen
14 spp.; widespread; Curran 1925*b*

86. Apical section of R_{4+5} at least three-quarters as long as crossvein h (as in Fig. 55) 87

Apical section of R_{4+5} not more than one-third as long as crossvein h (as in Fig. 49) (some species of *Blera* varying in this character, running out in either half of couplet) 93

87. Face mostly or entirely bright to dull yellow, at most obscurely darkened medially 88

Face black in background color, rarely slightly yellowish below 90

88. Abdomen either shining metallic or blackish with shining metallic bands, with brassy yellow hairs but without yellow markings .... **Hadromyia** (**Chrysosomidia** Curran)
5 spp.; widespread; Shannon 1916

Abdomen either black and at least partly black-haired or black with clear yellow markings on tergites 2–4 89

89. Abdomen entirely black, black-haired except for yellow-haired tergite 4. Middle femur of male with long ventral subbasal spur (Fig. 83). Large robust flies, mimicking bumblebees .... **Hadromyia** (**Hadromyia** Williston)
1 sp., *grandis* Williston; western

Abdomen black, usually with yellow lateral marks on at least tergites 2–4, always extensively pale-haired (Fig. 101). Middle femur of male simple. Flies not mimicking bumblebees .... **Blera** Billberg, in part
16 spp.; widespread; Curran 1953

90. Crossvein r-m situated slightly before middle of cell dm. Abdomen broadly oval. Ventral scutellar fringe present or absent. Male narrowly dichoptic .... **Lejota** Rondani, in part
see couplet 66

Crossvein r-m situated beyond middle of cell dm. Abdomen elongate. Ventral scutellar fringe present (as in Fig. 63). Male holoptic 91

91. Head triangular in anterior view (Fig. 37); face extensively shining; gena broad, much broader than posterior thoracic spiracle. First flagellomere kidney-shaped, wider than long (Fig. 26). Hind femur greatly enlarged, arcuate, with a small apicoventral tubercle frequently hidden by tibia .... **Brachypalpus** Macquart 92

Head elliptic in anterior view (Fig. 38); face pruinose; gena narrow, narrower than posterior thoracic spiracle. First flagellomere longer than wide. Hind femur not greatly enlarged or arcuate, without ventral tubercle .... **Xylota** Meigen
29 spp.; widespread; Shannon 1926*b*, Curran 1941 (as part of *Heliophilus*)

92. Face straight under antenna, with its lower margin produced strongly forward beyond level of base of antenna (Fig. 26) .... **Brachypalpus** (**Crioprora** Osten Sacken)
4 spp.; widespread; Williston 1887

Face concave, its lower margin not produced forward beyond level of base of antenna (Fig. 37) .... **Brachypalpus** (**Brachypalpus** Macquart)
1 sp., *oarus* (Walker); eastern

93. Ventral scutellar fringe present (as in Fig. 63). Face black in background color. Abdomen black, without pale markings 94

Ventral scutellar fringe absent or face partly yellow in background color. Abdomen often with yellow markings 95

94. Face concave, not produced forward below. Crossvein r-m situated beyond middle of cell dm. Large robust long-haired flies, mimicking bumblebees .... **Pocota** Lepeletier & Serville
1 sp., *bomboides* Hunter; western

Face tuberculate, produced strongly forward below (Fig. 23). Crossvein r-m situated before middle of cell dm (Fig. 49). Small slender short-haired flies, not mimicking bumblebees.... .... ***Cynorhinella*** Curran, in part

see couplets 66 and 79

95. Abdomen black, with three pairs of large yellow spots. Wing with anterior margin brown; crossvein r-m situated at outer third of cell dm. Frontal prominence strong, distinct (Fig. 27).... .... ***Somula*** Macquart

2 spp.; eastern; Curran 1925*b*

Abdomen black, without large yellow spots; sides or basolateral angles of tergites sometimes yellow (Fig. 101) or apical tergites sometimes red. Wing hyaline or uniformly brownish; crossvein r-m at most situated slightly beyond middle of cell dm. Frontal prominence weak.. ***Blera*** Billberg, in part

see couplet 89

96. Apical portion of M_1 curved strongly toward wing base (Fig. 56) 97

M_1 outwardly oblique (Fig. 52) 99

97. Anterior anepisternum haired (as in Fig. 65). Long-haired flies, mimicking bumblebees ... . ***Volucella*** Geoffroy

1 sp., *bombylans* (Linnaeus); widespread

Anterior anepisternum bare. Short-haired flies, not mimicking bumblebees 98

98. Face with median and lateral tubercles (Fig. 28). Posterior half of anepimeron haired; notopleuron greatly enlarged and produced posteriorly. Wing membrane without microtrichia. Metallic green or purple species .... ***Ornidia*** Lepeletier & Serville

1 sp., *obesa* (Fabricius); southern

Face with median tubercle only. Posterior half of anepimeron bare; notopleuron not enlarged. Species usually not metallic, but if so, then wing membrane extensively trichose .... ***Copestylum*** Macquart

39 spp.; widespread; Curran 1930*c*, 1935, 1939*a* (as part of *Volucella* and as *Volucellosia* Curran)

99. Eye and face densely haired (Fig. 31) .... ***Pyritis*** Hunter

2 spp.; western; Osburn 1904

Eye bare; face on lower half haired only laterally along eye margin 100

100. Metasternum bare; ventral scutellar fringe absent .... ***Brachyopa*** Meigen....101

Metasternum haired; ventral scutellar fringe present (as in Fig. 63) 102

101. Apical section of R_{4+5} longer than crossvein r-m. Hind tibia with short strong black spines on anterior surface. Anepisternum, postalar callus, and scutellum with strong bristles. Face of male with tubercle .... ***Brachyopa*** (***Hammerschmidtia*** Schummel)

1 sp., *ferruginea* Fallén; widespread

Apical section of R_{4+5} shorter than crossvein r-m (Fig. 52). Hind tibia without spines. Thorax with at most very weak bristles. Face of male without tubercle .... ***Brachyopa*** (***Brachyopa*** Meigen), in part

see couplet 70

102. Face usually entirely black or brownish black. If face orange medially, then anepisternum or notopleuron or both with bristles. Abdomen dark, without yellow markings .... ***Hiatomyia*** Shannon

22 spp.; widespread; Hull and Fluke 1950

Face usually entirely yellow. If face yellow with black median stripe, then thorax without bristles. Abdomen usually with yellow markings 103

103. Apical portion of M_1 curved toward wing base (Fig. 57). Anterior anepisternum haired (as in Fig. 65). Hind femur with apicoventral flange .... ***Merodon*** Meigen

1 sp., *equestris* (Fabricius); widespread

M_1 outwardly oblique (Figs. 58–60). Anterior anepisternum bare. Hind femur without such a flange..104

104. Cell r_{2+3} open to wing margin (Figs. 58, 59) 105

Cell r_{2+3} closed before wing margin (Fig. 60)..................................116

105. Arista plumose (as in Fig. 31) 106

Arista bare 107

106. Abdomen with yellow markings, or, if entirely black, tergites 2–4 entirely black-haired. Body short-haired. Flies not mimicking bumblebees .... ***Sericomyia*** Meigen

11 spp.; widespread, including Arctic; Curran 1934

Abdomen entirely black, with some or all of tergites 2–4 red- or yellow-haired. Body with longer hairs. Flies mimicking bumblebees .... ***Arctophila*** Schiner

2 spp.; western; Osburn 1908

107. Lower two-thirds of face haired only lateral to frontogenal suture; male holoptic; face of female concave. Hind femur without anterior basal patch of short dense black setulae. Apical section of A_1 elongate, sometimes not reaching wing margin (Fig. 55) 108

Lower two-thirds of face haired medial to frontogenal suture, usually with only a narrow median stripe bare (Figs. 32, 33); male holoptic or dichoptic; face of female tuberculate or straight. Hind femur with anterior basal patch of short dense black setulae (as in Fig. 89). Apical section of A_1 short, curved abruptly toward wing margin just beyond apex of cell cu*p* (Figs. 58, 59) 109

108. Metasternum haired. Apical section of A_1 long, straight, not reaching wing margin (Fig. 55). Hind tibia of male with strong ventral spur (Fig. 90) .... ***Teuchocnemis*** Osten Sacken, in part

see couplet 81

Metasternum bare. Apical section of A_1 turned caudally to reach wing margin. Hind tibia of male simple, without spur .... ***Pterallastes*** Loew

1 sp., *thoracicus* Loew; eastern

109. Wing membrane partly bare on basal third. Eye bare or haired. Scutum not striped. Abdomen dark, without pale markings. Long-haired flies, mimicking bumbleblees or other hairy bees (Fig. 3) .... ***Mallota*** Meigen

9 spp.; widespread; Curran 1940

Wing membrane entirely covered with microtrichia. Eye bare. Scutum usually with longitudinal stripes. Abdomen usually with pale markings. Short-haired flies, not mimicking hairy bees 110

110. Pterostigma elongate, not simulating a crossvein, at most slightly darkened basally (Fig. 58). Abdomen oval, with large orange markings on at least tergite 2 .... ***Helophilus*** Meigen

10 spp.; widespread, including Arctic; Curran and Fluke 1926

Pterostigma very short, simulating a crossvein (Fig. 59). Abdomen oval to slender, variable in color 111

111. Face pale, yellow to orange in background color and completely pale pruinose 112

Face mainly black in background color, pale pruinose laterally but shining black medially 113

112. Hind tibia produced apicoventrally as an acute or rounded spur, with ventral knife-edged carina on basal half; carina continuing less distinctly posteroventrally to or almost to tibial apex (Fig. 91) .... ***Lejops*** (***Anasimyia*** Schiner)

10 spp.; widespread; Curran and Fluke 1926 (as *Lejops* Rondani and *Eurimyia* Bigot)

Hind tibia truncate apically, with ventral carina restricted to basal half and with apical half rounded below (Fig. 92) .... ***Parhelophilus*** Girschner

8 spp.; widespread; Curran and Fluke 1926

113. Male with hind femur enlarged, arcuate, with basal and subapical ventral tubercles; hind tibia arcuate and produced into a long apical spur (Fig. 85). Female with sternites 1 and 3 swollen; sternite 1 overlapping sternite 2; sternite 2 reduced, sunken, membranous medially (Fig. 93) .... ***Lejops*** (***Polydontomyia*** Williston)

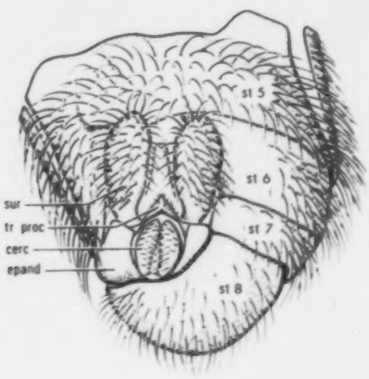
1 sp., *curvipes* (Wiedemann); widespread

Male without ventral femoral tubercles or apical tibial spur. Female with normal flat abdominal sternites 114

114. Ocellar triangle very large; posterior ocelli closer to eye margins than to midpoint between them (Fig. 39). Abdomen partly reddish in background color or with pairs of white pruinose arcuate spots, or both .... ***Lejops*** (***Asemosyrphus*** Bigot)

1 sp., *polygrammus* (Loew); western

Ocellar triangle small; posterior ocelli not closer to eye margins than to midpoint between them. Abdomen black, without white pruinose arcuate spots 115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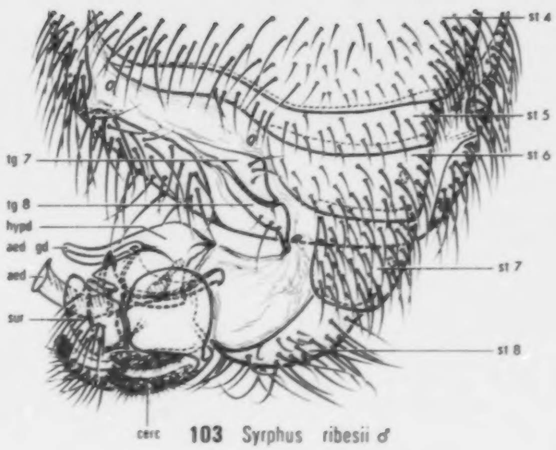
102 Toxomerus geminatus ♂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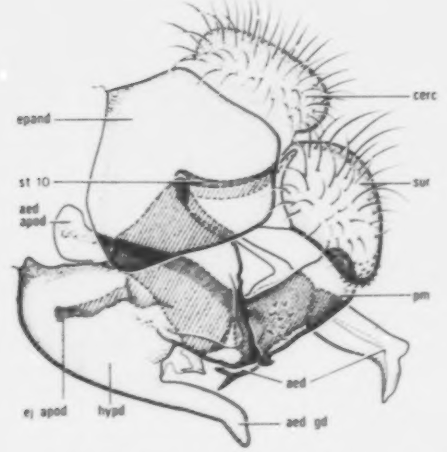
103 Syrphus ribesii ♂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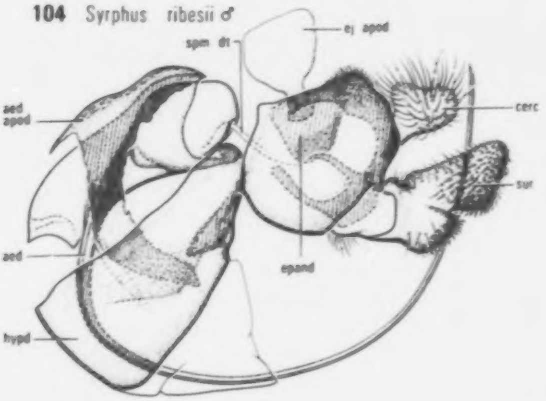
104 Syrphus ribesii ♂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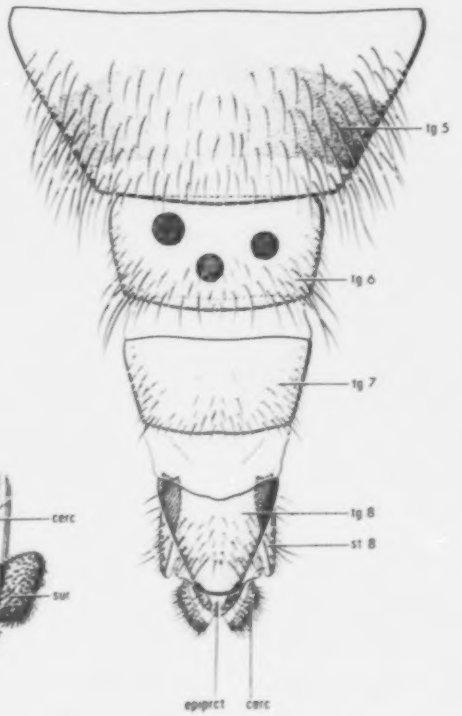
105 Microdon manitobensis ♂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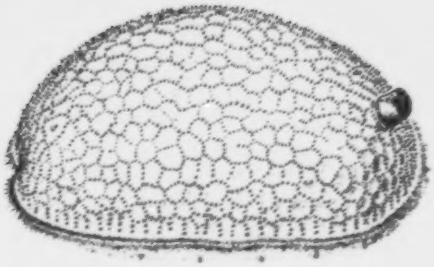
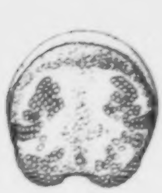
106 Syrphus ribesii ♀

Figs. 52.102–106. Apices of abdomen and terminalia: ventral views of apex of male abdomen and terminalia of (102) *Toxomerus geminatus* (Say) and (103) *Syrphus ribesii* (Linnaeus) (with terminalia exposed); lateral views of male terminalia of (104) *Syrphus ribesii* and (105) *Microdon manitobensis* Curran; (106) dorsal view of female terminalia of *Syrphus ribesii*.

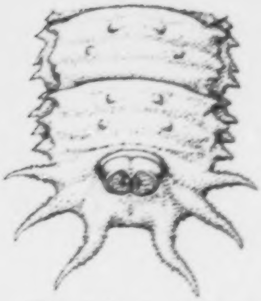
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; hypd, hypandrium; pm, paramere; spm dt, sperm duct; st, sternite; sur, surstylus; tg, tergite; tr proc, triangular process.



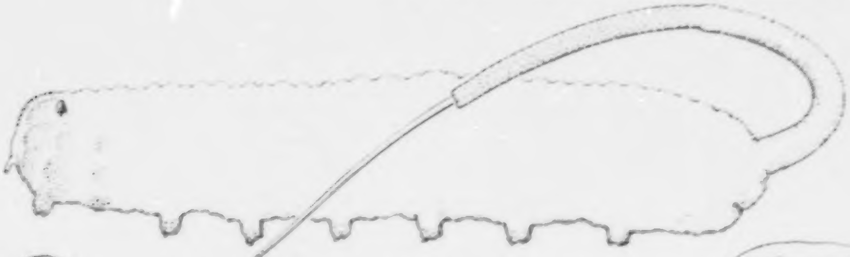
107 Microdon ruficrus



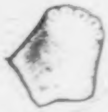
108 Microdon ruficrus



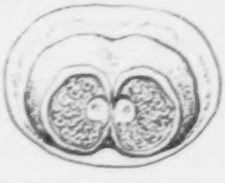
109 Volucella bombylans



111 Eristalis (Eristalis) tenax

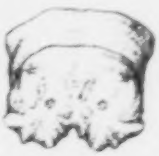


110 Syrphus knabi

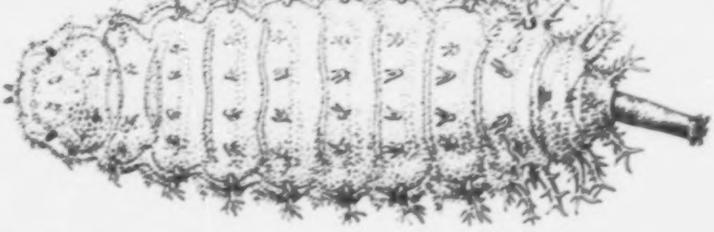


112 Volucella bombylans

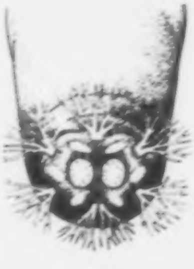
113 Syrphus knabi



114 Syrphus knabi



115 Brachyopa sp.



116 Brachyopa sp.

Figs. 52.107–116. Larvae: (107) *Microdon ruficrus* Williston, dorsolateral view; (108) terminal spiracles of *Microdon ruficrus*; (109) dorsal view of last three segments of *Volucella bombylans* (Linnaeus); (110) anterior spiracle of *Syrphus knabi* Shannon; (111) lateral view of *Eristalis (Eristalis) tenax* (Linnaeus); (112) spiracles of *Volucella bombylans*; (113) lateral view of *Syrphus knabi*; (114) terminal spiracles of *Syrphus knabi*; (115) dorsal view of *Brachyopa* sp.; (116) terminal spiracles of *Brachyopa* sp.

115. Face produced anteroventrally, almost straight, without distinct tubercle (Fig. 32). Length 10 mm or more .... ***Lejops*** (***Arctosyrphus*** Frey)

1 sp., *willingii* (Smith); boreal

Face not produced anteroventrally, with large distinct tubercle (Fig. 33). Length 8 mm or less .... ***Lejops*** (***Lunomyia*** Curran & Fluke)

1 sp., *cooleyi* (Seamans); central Nearctic

116. Metasternum bare. Hind femur without basal patch of black setulae .... ***Palumbia*** Rondani

1 sp., *inflata* (Macquart); doubtfully Nearctic; Thompson 1975

Metasternum haired (as in Fig. 76). Hind femur with basal patch of dense black setulae (Fig. 89) 117

117. Katepimeron, posterior half of anepimeron, meron, and metepisternum all bare 118

Katepimeron haired; other sclerites mentioned above frequently partly haired 119

118. Eye bare. Scutum with patches of yellow tomentum .... ***Meromacrus*** Rondani

4 spp.; southern; Hull 1942*b*

Eye haired. Scutum without patches of yellow tomentum .... ***Eristalis*** (***Eoseristalis*** Kanervo)

17 spp.; widespread; Curran 1930*a*, Telford 1970 (both as part of *Eristalis*)

119. Eye with dark spots. Triangular portion of anepimeron below wing base haired (Fig. 64); postalar ridge with tuft of strong black hairs (Fig. 78) .... ***Eristalinus*** Rondani

1 sp., *aeneus* (Scopoli); widespread

Eye unicolorous. Triangular portion of anepimeron below wing base bare; postalar ridge bare 120

120. Meron bare, without hairs in front of or below posterior spiracle. Arista with short but distinct hairs on basal half. Eye densely haired, with two vertical bands of longer hairs. Wing membrane without microtrichia .... ***Eristalis*** (***Eristalis*** Latreille)

1 sp., *tenax* (Linnaeus); widespread

Meron with fine pale hairs in front of or below spiracle. Arista bare. Eye haired above, without contrasting bands of longer hairs. Wing membrane with or without microtrichia .... ***Palpada*** Macquart

10 spp.; central U.S.A. southward; Curran 1930*a*, Telford 1970 (both as part of *Eristalis*)

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PIPUNCULIDAE

53

D. E. Hardy

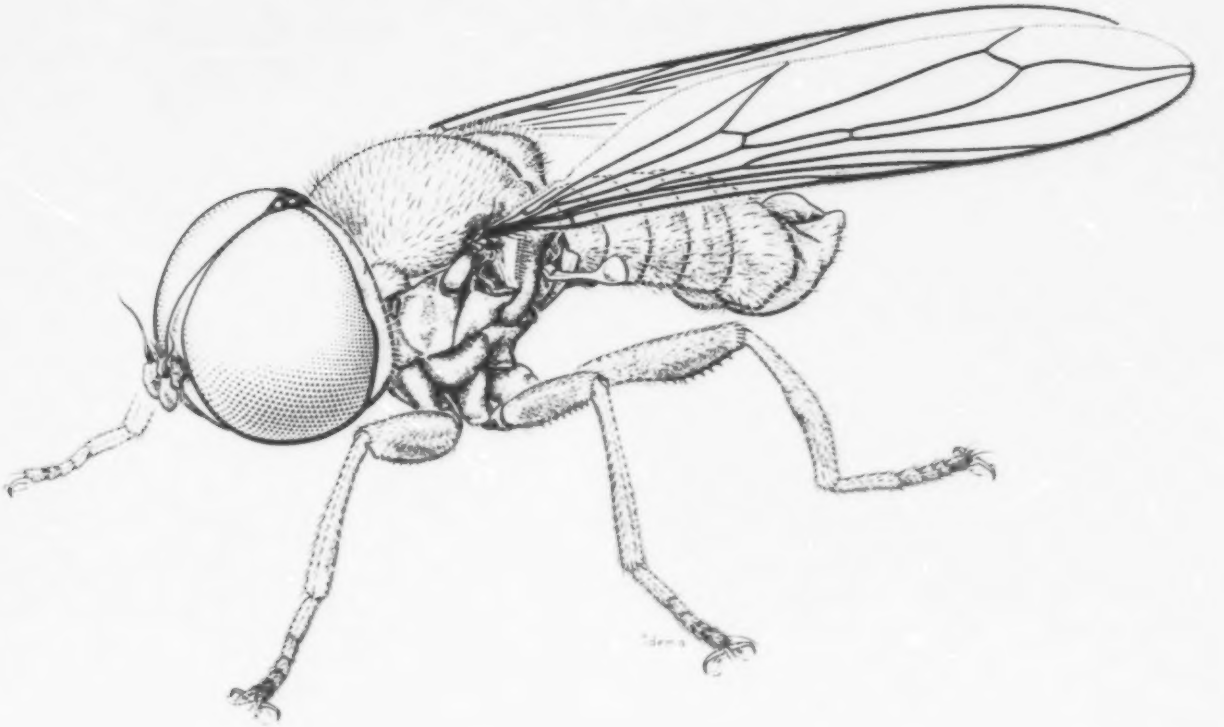


Fig. 53.1. Male of *Pipunculus ater* Meigen.

Rather small typically dark-bodied flies, 3.4–4.0 mm long, characterized by globose to semiglobose compound eyes covering almost entire head (Fig. 1). Wing typically long and slender.

Adult. Head: hemispherical (Chalarinae) to nearly spherical (Pipunculinae) (Fig. 7). Ocellar bristles present and occiput very narrow in Chalarinae; ocellar bristles lacking and occiput generally swollen and plainly visible in Pipunculinae. Eyes of male usually contiguous on frons, but dichoptic in Chalarinae, *Nephrocerus* Zetterstedt, *Dorylomorpha* Aczél, and a few species of *Pipunculus* Latreille. Antenna three-segmented; scape very short, inconspicuous; pedicel usually higher than long, with prominent ventral and dorsal setae; first flagellomere varying from short and obtusely pointed to long and acuminate ventrally; arista dorsal, divided into three aristomeres; apical aristomere thickened at base, long and tapering to apex. Mouthparts typically muscoid; palpus small, inconspicuous, microscopically annulated, with no apparent segmentation, with an apical sensory vesicle and one or more fine apical setae.

Thorax: typically shining black, pruinose in varying degrees; pruinescence in the form of fine inconspicuous pile dorsally along dorsocentral lines and along sides or short hairs scattered over disc (Pipunculini), rather dense pile (Chalarinae), or prominent marginal bristles on scutum and scutellum (Nephrocerini). Proepisternum usually hidden by expanded occiput and sometimes bearing a fan-like tuft of hairs; postpronotum varying from pale yellow to black. Legs usually simple; trochanters often ornate in *Tomosvaryella* Aczél; femora usually with rows of small spines ventrally toward apices, and often with anterior or posterior setae; front tibia sometimes with ventral bristles at apex; hind tibia often with strong erect anterior setae medially; claws and pulvilli moderately large. Wing (Figs. 2–6) hyaline to faintly infuscated, iridescent in direct light, typically slender, rather elongate, as long as or longer than body; calypter and anal lobe weak; pterostigma present or absent. Venation varying among genera and subgenera, but Sc rather long and complete; Rs two-branched; R_{2+3} and R_{4+5} divergent; R_{4+5} and M_1, when present, terminating close together in C; M one- or two-branched; M_2 when present very short; CuA_2 fused with A_1 just before wing margin; cell cup always long and acutely pointed; crossvein r-m variable in position; cell R_{4+5} open in wing margin. Calypteres small and narrow. Halter varying from pale yellow to black.

Abdomen: variable in shape but typically subcylindrical (Figs. 8, 9), rounded at sides, broadest at about segment 3, and varying from densely pruinose, velvety opaque, subshining, to highly polished. Tergite 1 often with a row of bristles on each side.

In male (Fig. 8), segments beyond segment 5 twisted toward left; in some groups tergites 6 and 7 positioned laterally or ventrally. Syntergosternite 8 often large, located at apex of abdomen; epandrium and surstyli positioned ventrally and folded against genital chamber; aedeagus and associated structures enclosed within cavity of syntergosternite 8 and visible only in completely cleared specimens or when dissected out. Development of syntergosternite 8 as seen in situ and shape of surstyli seen from ventral view important for species differentiation. Cercus small but distinct.

In female (Fig. 9), ovipositor (piercing organ) well-adapted for inserting eggs into body of host, and composed of modified abdominal segments 7, 8, and 9; tergite 7 slender, heavily sclerotized, forming base of ovipositor and containing spiracle 7; tergite 8 large; tergite 9 reduced; entire ovipositor folded beneath abdomen in normal position. Anal opening situated on dorsum of ovipositor near junction with base; cercus small but conspicuous because of fringe of moderately long setae. Genital opening located on venter of ovipositor, usually situated in a thickened portion near base of piercer. Three sclerotized spermathecae present, important taxonomically (Harris 1966) and probably phylogenetically, varying in shape from spherical to reniform, to filiform, and tubular.

Larva. Oblong, rounded at ends, slightly more pointed anteriorly (Fig. 10). Integument wrinkled obscuring segmentation, but 10 or 11 segments apparently present. Larva amphipneustic, with only anterior and posterior pairs of spiracles open; anterior spiracles located near sides, usually just posterior to mandibles; posterior pair of spiracles situated on a sclerotized plate located dorsomedially just before apex of abdomen; two or three openings present in posterior spiracles of mature larva, but three apparently more common. Arrangement of spiracles and processes of sclerotized plates as well as structures of mandibles apparently useful for separation of species in larval stage. Only two larval instars are known for the family (Jervis 1980).

Pupa. Puparium oblong, broadly rounded at ends, varying from reddish brown to black. Integument usually roughened, often wrinkled, sometimes appearing sculptured, and occasionally covered with sparse hairs and long strong spines (Ott 1900); whorls of erect bristly hairs borne on each spine. Pupal respiratory horns projecting through weakened areas of integument at anterior margins of abdominal segment 1 and positioned dorsolaterally, usually small, slender, and rather inconspicuous but in some species well-developed and sometimes bearing apical processes; posterior spiracles similar to those of larva. General features of puparium carried over from mature larva, including larval vestiture. Upon emergence of adult, anterior portion of puparium (operculum) pushed off and case broken into pieces along definite lines of fracture; according to Coe (1966*a*) operculum apparently consisting of two detached pieces in most Pipunculidae and of five pieces in *Chalarus* Walker and *Verrallia* Mik.

Biology and behavior. The biology and immature stages of Pipunculidae are poorly known, because only a few species have been studied (Jervis 1980). Careful work is needed to gain a better knowledge of these flies. Pipunculidae are endoparasites of various families of Homoptera, especially Cicadellidae and Delphacidae, and are important as biological control agents. The adults are frequently seen hovering in and over vegetation; their flight is similar to that of Syrphidae. The females search out nymphs of leafhoppers and other Homoptera as hosts in which to deposit their eggs. They snatch their prey with their legs and hold them in their strong tarsal claws. While in flight they insert the egg into the host through the conjunctiva between the abdominal segments. The larva develops to maturity within the host, and at full size it fills the entire body cavity. After escaping from the host, the larva drops to the ground and pupates in the soil, in ground litter, at the bases of plants, or in crotches of trees.

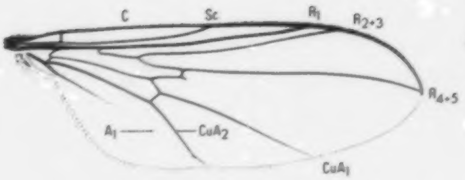
Classification and distribution. The most recent monograph of the Nearctic species was by Hardy (1943). At present, 105 species and 9 subspecies are known from the Nearctic region. Approximately 600 species are known from the entire world. The handbook of the British species by Coe (1966*a*) is a useful reference. The larval morphology has not been worked out in detail. The cephalopharyngeal skeleton is well developed, and the development of this structure is clearly important taxonomically. To date, no one has attempted to set up a classification based on the larvae.

Six fossil species are known, one from the Miocene deposits of Florissant, Colo., and five from Baltic amber of the Oligocene age. These specimens belong in four extant genera: *Protonephrocerus* Collin, *Verrallia* Mik, *Nephrocerus* Zetterstedt, and *Pipunculus* (*Cephalosphera* Enderlein). All exhibit the primitive forking of M_{1+2}; in *Protonephrocerus collini* Carpenter & Hull, M_2 extends to the wing margin (Carpenter and Hull 1939).

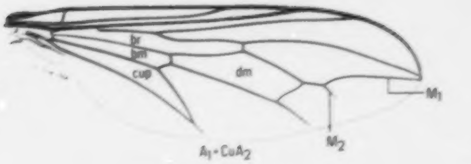
Key to genera

1. Ocellar bristles present; occiput narrow, scarcely visible from lateral view. Species rather densely pilose . . . . CHALARINAE 2

Ocellar bristles lacking; occiput swollen and plainly visible in lateral view (Fig. 7). Species usually not densely haired . . . . PIPUNCULINAE 4


C
Sc
R1
R2+3
R4+5
A1
CuA2
CuA1

2 Chalarus spurius ♂


br
bm
cup
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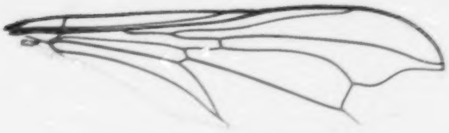
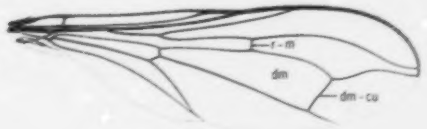
A1+CuA2
M2

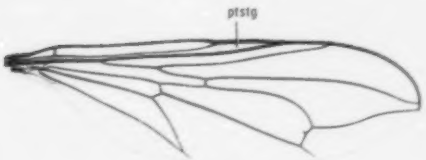
3 Verrallia aucta ♂



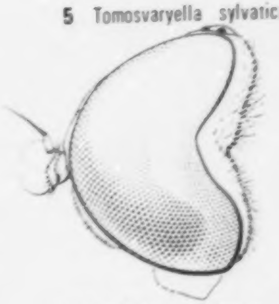
4 Dorylomorpha exilis ♂



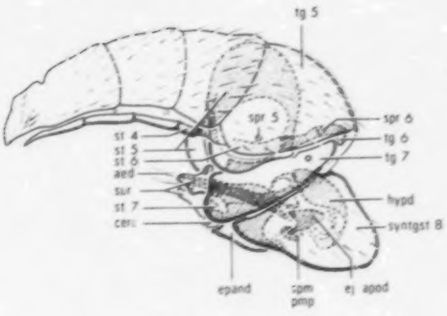
5 Tomosvaryella sylvatica ♂



6 Pipunculus fuscus ♂



7 Nephrocerus daeckei ♂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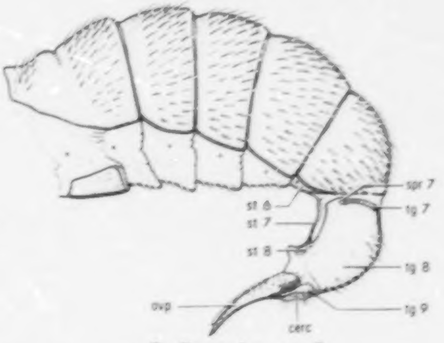
8 Dorylomorpha canadensis ♂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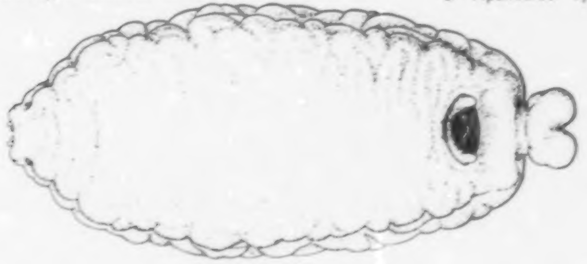
9 Pipunculus sp. ♀



10 Pipunculus sp.

Figs. 53.2–10. Wings, head, abdomens, and larva: wings of (2) *Chalarus spurius* (Fallén), (3) *Verrallia aucta* (Fallén), (4) *Dorylomorpha exilis* (Malloch), (5) *Tomosvaryella sylvatica* (Meigen), and (6) *Pipunculus fuscus* Loew; (7) head of *Nephrocerus daeckei* Johnson; abdomens of (8) male of *Dorylomorpha canadensis* Hardy and (9) female of *Pipunculus* sp.; (10) larva of *Pipunculus* sp.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; hypd, hypandrium; ovp, ovipositor; ptstg, pterostigma; spm pmp, sperm pump; spr, spiracle; st, sternite; sur, surstylus; syntgst 8, syntergosternite 8; tg, tergite.

2. Wing venation complete: cell dm closed (Fig. 3) .... ***Verrallia*** Mik....3

Wing venation with most of medial veins and crossvein dm-cu lacking (Fig. 2) .... ***Chalarus*** Walker

2 spp.: introduced. Palaearctic, possibly cosmopolitan; Coe 1966*a* and 1966*b*, Hardy 1943

3. M_2 present as a short stump vein beyond crossvein dm-cu (Fig. 3) .... ***Verrallia*** (***Verrallia*** Mik)

2 spp.: introduced and possible native. Washington, South Dakota to Virginia and Massachusetts; Coe 1966*a*

M_2 absent .... ***Verrallia*** (***Jassidophaga*** Aczél)

2 spp.: introduced and native. Colorado and New Mexico, and Quebec to New Jersey; Coe 1966*a*, Hardy 1943

4. Hind margin of eye straight or nearly so. Thorax lacking bristles. First flagellomere usually pointed ventrally .... PIPUNCULINI....5

Hind margin of eye deeply excised medially (Fig. 7). Margins of scutum and scutellum with strong bristles. First flagellomere reniform, rounded ventrally .... NEPHROCERINI....***Nephrocerus*** Zetterstedt

2 spp.: northeast; Hardy 1943

5. Pterostigma absent (Fig. 5); no pigmentation at apex of cell sc 6

Pterostigma present (Fig. 6) 7

6. Abdomen in both sexes rather clavate in shape, swollen posteriorly; male terminalia large and conspicuous (Fig. 8). Eyes of male dichoptic. Crossvein r-m situated near base of cell dm (Fig. 4) .... ***Dorylomorpha*** Aczél

9 spp., widespread; Hardy 1943

Abdomen in both sexes widest at about junction of segments 3 and 4, slightly tapering posteriorly; male terminalia not wider than abdominal segment 5. Eyes of male contiguous for at least a short distance on frons (as in Fig. 1). Crossvein r-m usually near middle of cell dm (Fig. 5) .... ***Tomosvaryella*** Aczél

34 spp., 1 subsp.; widespread; Hardy 1943 (=*Allomethus* Hardy)

7. M_2 present as a short stump vein beyond crossvein dm-cu (as in Fig. 3) .... ***Cephalosphaera*** Enderlein

8 spp., widespread; Hardy 1943

M_2 absent (Fig. 6) 8

8. Proepisternum with a fan-like tuft of fine hairs .... ***Pipunculus*** Latreille....9

Proepisternum bare .... ***Pipunculus*** (***Eudorylas*** Aczél)

36 spp., 4 subspp.; widespread; Hardy 1943

9. Anterior portion of scutum evenly setose; dorsocentral hairs not differentiated .... ***Pipunculus*** (***Pipunculus*** Latreille)

6 spp., 3 subspp., widespread; Hardy 1943, Coe 1966*a*

Scutum with a row of fine setae down each dorsocentral line, with area between these lines bare .... ***Pipunculus*** (***Cephalops*** Fallén)

4 spp., 1 subsp.; widespread; Hardy 1943, Coe 1966*a*

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CONOPIDAE

54

KENNETH G. V. SMITH AND B. V. PETERSON

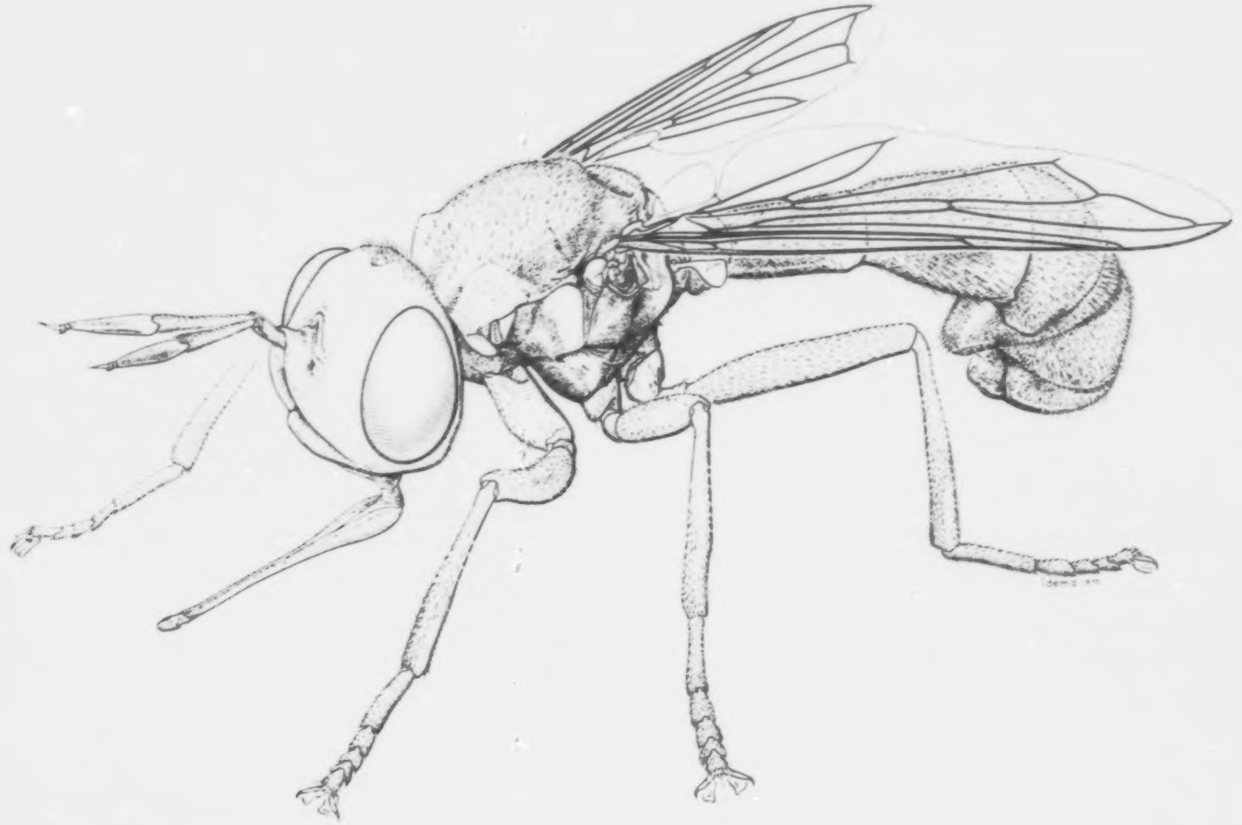


Fig. 54.1. Female of *Physoconops brachyrhynchus* (Macquart).

Rather bare and elongate flies (Fig. 1), 3.0–20.0 mm long, usually pruinose, and colored black and yellow, reddish brown, or blackish, often with striking resemblance to solitary wasps and other Hymenoptera. Head broad; proboscis usually long, singly or doubly geniculate. Wing spotted or unmarked, or with a band along costal margin; cell r_{4+5} closed or nearly so.

Adult. Head: rather large (Figs. 2–4), broader than thorax. Frons broad, widely separating eyes in both sexes. Eye bare; in *Stylogaster* Macquart anteromedial facets enlarged, often considerably so, especially in female (Fig. 3); ocelli usually absent (Conopinae) or present (other subfamilies). Occiput and vertex with short hairs; vertical bristles present or absent, very well-developed in *Stylogaster*. Occiput more or less inflated. Subcranial cavity large. Proboscis long, sometimes very long, slender, projecting horizontally forward or downward, geniculate at base only (Fig. 2) (Conopinae and *Zodion* Latreille) or at base and middle (Figs. 3, 4) (Myopinae except *Zodion*, Dalmanniinae, and Stylogasterinae); palpus present or absent, when present varying in length and shape, cylindrical or clavate. Antenna porrect, three-segmented; first flagellomere generally elongate with a short apical three-segmented stylus (Conopinae, Fig.7), or shorter and with a dorsal two- or three-segmented arista (other subfamilies, Fig. 6).

Thorax: subquadrate, rather bare; short setae usually present on scutum; bristles not well-developed but postpronotal, katepisternal, notopleural, supra-alar, and postalar bristles often present; strong prescutellar dorsocentral bristles and a strong anepimeral bristle present in *Stylogaster*; well-developed proepisternal bristle present in *Stylogaster* and Conopini; marginal bristles usually weak on scutellum, but these strong in *Stylogaster*. Scutellum semicircular. Wing (Figs. 8–13) of moderate length and width, slightly shorter to slightly longer than abdomen, cuneiform at base in *Stylogaster* (Fig. 10); membrane hyaline or patterned in some genera; a short but distinct crossvein sc-r (wrongly termed Sc_2 by most previous authors) present near tip of Sc in some genera; R_{4+5} and M_{1+2} strongly convergent apically and sometimes fused distally; cell r_{4+5} narrowly open (Figs. 11, 13), or closed at margin, or short petiolate (Figs. 8, 9, 10, 12); spurious vein (called M_1 by most previous authors), similar to that of Syrphidae, present in some genera, extending distally from crossvein r-m and usually running close to R_{4+5} or M_{1+2}; cell br about twice as long as cell bm; crossvein dm-cu situated relatively close to apex of CuA_1; CuA_2 fused with A_1 so that cell c*up* is always closed and petiolate, often elongate (Figs. 8, 9, 12, 13) but shorter in *Dalmannia* Robineau-Desvoidy (Fig. 11), and shorter than cell bm in *Stylogaster* (Fig. 10); CuP rather short but often distinct; A_1 strong; A_2 variably distinct; calypteres small. Legs moderately long, without distinct bristles, usually almost bare, of uniform shape except for thickening of femora in some genera, e.g. *Physocephala* Schiner (Fig. 5); mid coxal prong absent; mid tibia, at least, usually with a small preapical dorsal bristle; claws long and slender; pulvilli pad-like, distinct; empodia usually long, slender, and bristle-like but greatly reduced and hair-like in at least some *Stylogaster*.

Abdomen: cylindrical, more or less clavate (Figs. 14–17), sometimes broad basally and sometimes slender and markedly constricted at base, sometimes distinctly curving downward posteriorly (Fig. 15), sparsely haired or almost bare, and usually more or less pruinose. Seven pairs of spiracles present in both sexes.

Female abdomen with seven distinct segments; segment 7 not forming an ovipositor sheath as in many other Schizophora. Tergites 6, 7, and 8 variously reduced or enlarged; tergite 7 sometimes enlarged and capsule-like; tergites 8 and 9 usually fused (Figs. 16, 17) but when discernible usually faintly demarcated, often bearing a spine-like process posteroventrally on each side that articulates with sternite 8. Cercus variously developed but discernible if small. Sternites variously developed and distinct; sternite 5 often enlarged and produced ventrally as a pad-like structure anteriorly and with a variously developed plate-like portion posteriorly; sternite 6 often similarly developed but with pad-like anterior portion usually smaller and with plate-like posterior portion usually larger than those in segment 5; pad-like processes of sternites 5 and 6 variously termed apophase copulatrice, unpaarige organ, theca, and ventral genital plates or processes; sternites 7 and 8 distinct; sternite 7 plate-like, sometimes with a double patch of setae posteriorly; sternite 8 sometimes rather well-developed and bearing a pair of small (*Stylogaster*) or large lobe-like processes; sternite 9 usually represented by an internal, variously developed, and variously sclerotized slender U-shaped structure; sternites 5, 6, and 8 often covered by various arrangements of spinules and setae of varying lengths; however, sternites 5 and 6, when not pad-like, often with tufts of setae and bristles. Posterior abdominal segments produced as a short but well-developed sclerotized ovipositor in *Dalmannia* (Fig. 17) and as a very elongate membranous one in *Stylogaster* (Fig. 15). Four sclerotized or unsclerotized spermathecae present in Conopinae and Myopinae; two sclerotized spermathecae present in Dalmanniinae and Stylogasterinae; spermathecae small and subspherical in all subfamilies except Stylogasterinae, in which they are larger and of various shapes.

Male abdomen shorter than that of female. Tergites 1–5 unmodified; tergite 6 represented by a narrow strip extending dorsally from sternite 6 and fused with tergite 7 into a single syntergosternite with elements of segment 8 and bearing spiracles 6 and 7. Segment (sternite) 8 often represented by a slender strip along posterior margin of this syntergosternite and often demarcated by a faint transverse furrow; sternites 1–4 unmodified; sternite 5 simple or somewhat enlarged, usually studded with a series of short spines and setae of varying lengths; sternites 6 and 7 variably developed; sternite 6, and sometimes 7, articulating with its respective tergite; sternite 7 sometimes reduced and rod- or plate-like and sometimes apparently absent. Epandrium well-developed (Fig. 18); surstylus, when present, variable in size, shape, and ornamentation, with spinules and setae; occasionally (*Zodion abitus* Adams) a small lobe-like process present anteroventral to surstylus that might represent an anterior surstylus; surstylus absent or greatly reduced in some genera. Cercus well-developed; hypoproct greatly reduced or absent, occasionally present as two short setose lobes. Sternite 10 varying in degree of sclerotization, size, shape, and ornamentation. Hypandrium Y-shaped, usually well-developed; gonopod, when present, greatly reduced; aedeagus rather short, with apex varying from a large membranous complex lobe-like structure to long and coiled with two rows of hairs in *Dalmannia*, to fusiform in *Myopa* Fabricius, to slender and tapering with a stiff central spine in *Zodion*, to slender and bifilamentous in some *Stylogaster*; base of aedeagus usually stout; sperm pump strongly developed in some genera, with an ejaculatory apodeme that varies in size and shape; aedeagal apodeme variable in length but usually well-developed. Paramere, surrounding base of aedeagus, usually heavily sclerotized, with short to long and variably shaped digitiform to pad-like extensions projecting on each side of aedeagus, and sometimes bearing spinules and setae in various patterns.

Cole (1927), Steyskal (1957), and Griffiths (1972) gave brief descriptions of the terminalia of several members of the Conopidae, but their accounts are not always very clear. Stuckenberg's (1963) treatment of the terminalia of two species of *Stylogaster* from Madagascar is more like the interpretation given here.

Egg. Micropylar end with a stalk bearing terminal filamentous processes in Conopinae (Fig. 26), Myopinae (Fig. 27), and Dalmanniinae (Fig. 28). End opposite micropyle in Stylogasterinae (Fig. 25) pointed and armed with barbs for penetrating and remaining in host cuticle (Lopes 1937; Rettenmeyer 1961; Stuckenberg 1963; Smith 1966, 1967).

Larva. White, tapering anteriorly in first and second instars, rather strongly attenuated anteriorly in third instar, and adapted for feeding on thoracic contents through abdominal petiole of hymenopterous host, at least in *Thecophora* Rondani (Fig. 21) and *Physocephala* (Fig. 23) (Smith 1966, Smith and Van Someren 1970). Cuticle smooth, except for a covering of minute tubercles that is densest in dorsal and caudal regions and along anterior margins of dorsal thoracic segments. Cephalopharyngeal skeleton withdrawn into anterior end of body, with only tip of mandibles projecting; mandibles rather large, with a curved anterior hook; dental sclerite small, undivided; hypopharyngeal sclerite sometimes fused with tentoropharyngeal sclerite or these separate; tentoropharyngeal sclerite large, lightly tanned, narrowly excised posteriorly (*Physocephala*) or deeply excised posteriorly (*Thecophora*); other sclerites deeply tanned. Respiratory system amphipneustic in Old World genus *Sicus* Scopoli, but in all other genera only posterior spiracles present; anterior spiracles in *Sicus* fan-shaped, with about 35 openings; posterior spiracles (Figs. 20, 22, 24) small to rather large, hemispherical or reniform, with numerous protuberances each with many openings, or simply with groups of openings not situated on protuberances (*Sicus, Thecophora*); total number of openings varying from about 50 to more than 400; a small circular toothed process usually situated behind each posterior spiracle, but this spine-like in *Physocephala sagittaria* (Say) (Townsend 1935), and possibly used for rupturing air sacs of host (Clausen 1940). Two elongate distally tapering retractile vesicles projecting posteroventrally in *Zodion* into which tracheae extend (Figs. 19, 20) (Howell 1967); a smaller pair of these vesicles present in *Sicus*. Larvae of Stylogasterinae or Dalmanniinae not known.

Biology and behavior. The biology of the family has recently been summarized by Freeman (1966) for Nearctic species and Smith (1966, 1967, 1969) for world species. The known larvae of all Conopinae, Myopinae, and Dalmanniinae are internal parasites of aculeate Hymenoptera, which the ovipositing females attack in flight. The adults feed at flowers of several families, especially Compositae, Labiatae, and Umbelliferae. *Zodion fulvifrons* Say (Severin 1937), *Physocephala marginata* (Say), and *P. sagittaria* (Hüttinger 1974) apparently have minor economic importance as parasites of the honey bee (*Apis mellifera* Linnaeus). The Stylogasterinae are parasitic on cockroaches and calypterate Diptera; females are often seen hovering over the heads of marching columns of army ants and darting after their hosts that are fleeing from the ants' front ranks. Both sexes may be found feeding on flowers, particularly Labiatae. Adults hover as they suck the nectar, a habit to which their long proboscis is well adapted.

Because further research on biology, especially of the subfamily Stylogasterinae, will probably have to begin at the egg stage, a key to eggs is included. This key should be used with caution, however, because it is based on only the few species known, mainly European, and may break down when the eggs of more species from each genus are described.

Classification and distribution. The family is fairly distinct, with the exception of *Stylogaster*, for which Rohdendorf (1964) has proposed a separate family. Because the genus shares some characters with *Dalmannia*, we prefer to retain it in the Conopidae until the biology is more fully known.

The taxonomic state of the family is not satisfactory because of the past use of highly variable characters. Sufficient specimens of associated sexes are rarely available for study because of the scarcity of the family in the field. However, a revival of interest in the biology of the family and a more critical approach to its taxonomy are evident among modern workers, and the Nearctic species in particular are now in much better taxonomic order than before.

The family contains 45 world genera and some 800 species and is well represented in all the major zoogeographic regions except for the Arctic, Antarctic, and many of the Pacific islands. There are 9 genera and 66 species known from the Nearctic region.

Two fossil Conopidae have been described, *Palaeomyopa tertiaria* Meunier and *Palaeosicus loewi* Meunier, both from Tertiary Baltic amber (Meunier 1899, 1912, 1916). These fossil Conopidae have been restudied by Hennig (1966), who synonymized the two species and discussed their phylogenetic significance.

Keys to genera

Adult

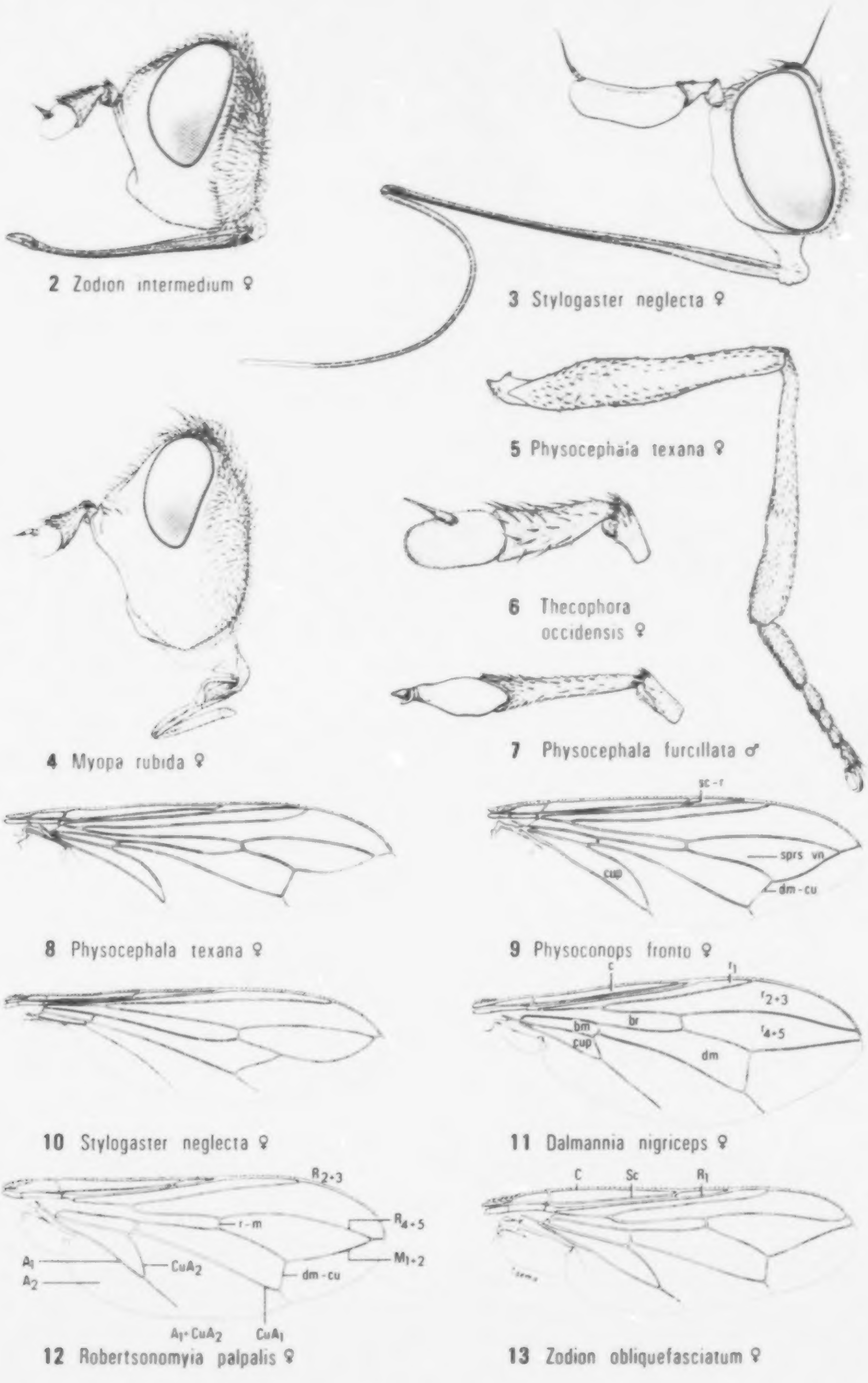
1. First flagellomere bearing an apical three-segmented stylus (Fig. 7). Ocelli usually absent, except in *Physoconops*. Abdomen constricted basally (Fig. 1) ....CONOPINAE....2

First flagellomere bearing a dorsal two- or three-segmented arista (Fig. 3). Ocelli present. Abdomen not noticeably constricted basally 6

2. Wing (Fig. 8) with crossvein r-m well beyond middle of cell dm. Ocelli absent. Proepisternum bare. Hind femur irregularly thickened on basal half (Fig. 5) ....PHYSOCEPHALINI....***Physocephala*** Schiner

7 spp.; widespread; Camras 1957

Wing (Fig. 9) with crossvein r-m at most a little beyond middle of cell dm. Ocelli usually present, vestigial, or rarely absent. Proepisternum with at least one bristle. Hind femur regularly thickened, thickest at middle ....CONOPINI....3


sc-r
sprs vn
cup
dm-cu
c
r1
r2+3
bm
br
r4+5
cup
dm
R2+3
r-m
R4+5
M1+2
A1
A2
CuA2
dm-cu
A1+CuA2
CuA1
C
Sc
R1

2 Zodion intermedium ♀

3 Stylogaster neglecta ♀

5 Physocephala texana ♀

6 Thecophora occidensis ♀

4 Myopa rubida ♀

7 Physocephala furcillata ♂

8 Physocephala texana ♀

9 Physoconops fronto ♀

10 Stylogaster neglecta ♀

11 Dalmannia nigriceps ♀

12 Robertsonomyia palpalis ♀

13 Zodion obliquefasciatum ♀

Figs. 54.2–13. Heads, leg, antennae, and wings: head of (2) *Zodion intermedium* Banks, (3) *Stylogaster neglecta* Williston, and (4) *Myopa rubida* (Bigot); (5) hindleg of *Physocephala texana* (Williston); antennae of (6) *Thecophora occidensis* (Walker) and (7) *Physocephala furcillata* (Williston); wings of (8) *Physocephala texana*, (9) *Physoconops fronto* (Williston), (10) *Stylogaster neglecta*, (11) *Dalmannia nigriceps* Loew, (12) *Robertsonomyia palpalis* (Robertson), and (13) *Zodion obliquefasciatum* (Macquart).

3. Vertex without an ocellar swelling. Proepisternum usually with more than one bristle at base. Abdominal segment 2 hardly constricted .... ***Conops*** **(*Asiconops*** **Chen)**

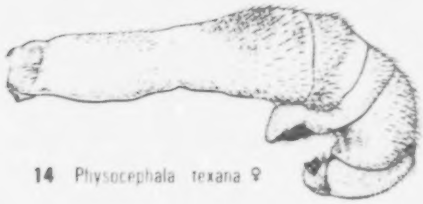
1 sp., *bermudensis* Parsons; Bermuda; Camras 1955

Vertex with a distinct ocellar swelling (Fig. 1). Proepisternum with one bristle at base. Abdominal segment 2 fairly long and narrow .... ***Physoconops*** Szilady....4

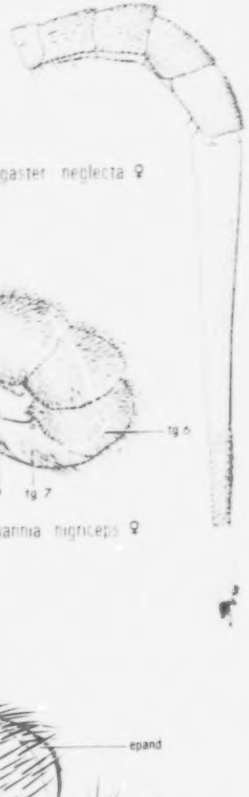
4. Frons as long as wide or longer. First flagellomere less than two-thirds length of pedicel .... ***Physoconops*** **(*Physoconops*** Szilady)

5 spp.; widespread; Camras 1955

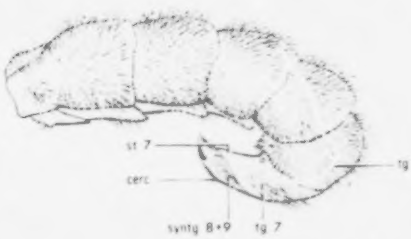
Frons shorter than wide. First flagellomere more than two-thirds length of pedicel (Fig. 1)....5



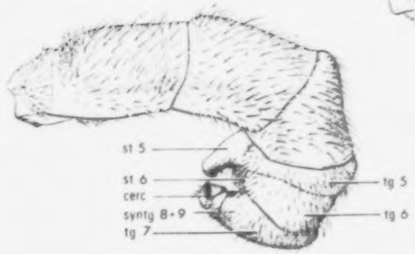
14 Physocephala texana ♀



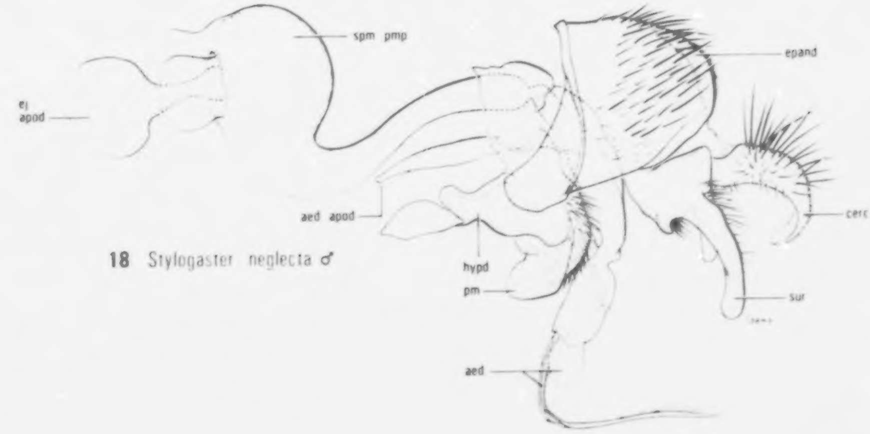
15 Stylogaster neglecta ♀



17 Dalmannia nigriceps ♀



16 Zodion perlongum ♀



18 Stylogaster neglecta ♂

Figs. 54.14–18. Abdomens and terminalia: abdomens of (14) *Physocephala texana* (Williston), (15) *Stylogaster neglecta* Williston, (16) *Zodion perlongum* Coquillett, and (17) *Dalmannia nigriceps* Loew; (18) male terminalia of *Stylogaster neglecta*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; hypd, hypandrium; pm, paramere; spm pmp, sperm pump; st, sternite; sur, surstylus; syntg, syntergite; tg, tergite.

5. Vertex large, as long as frons .... ***Physoconops*** (***Gyroconops*** Camras)
1 sp., *sylvosus* (Williston): California to Massachusetts south to Florida and Mexico

Vertex much shorter than frons (Fig. 1) .... ***Physoconops*** (***Pachyconops*** Camras)
6 spp.: widespread; Camras 1955

6. Wing with cell cu*p* long, much longer than cell bm (Figs. 12, 13). Female with a short ovipositor; sternite 5 with pad-like processes (theca) (Figs. 14, 16) .... MYOPINAE....8

Wing with cell cu*p* short (Figs. 10, 11). Female abdomen with an elongate ovipositor; sternite 5 without pad-like processes (theca) (Figs. 15, 17) 7

7. Face with a prominent median keel (Fig. 3). Wing with cell cu*p* shorter than cell bm (Fig. 10). Thorax and scutellum with distinct bristles. Female abdomen with a long membranous ovipositor (Fig. 15) .... STYLOGASTERINAE.... ***Stylogaster*** Macquart
2 spp.: midwestern and eastern U.S.A. and eastern Canada; Aldrich 1930, Curran 1942

Face deeply concave. Wing with cell cu*p* a little longer than cell bm (Fig. 11); crossvein bm-cu sometimes faint or absent so that cells bm and dm are coalesced. Thorax and scutellum with fine hairs only. Female with abdominal segments 7–10 shorter, sclerotized, strongly narrowed, and produced forward (Fig. 17) .... DALMANNIINAE.... ***Dalmannia*** Robineau-Desvoidy
6 spp.: widespread; Bohart 1938

8. Proboscis bent only once, near base (Fig. 2) 9

Proboscis doubly bent, once near base and once near middle (Figs. 3, 4) 10

9. Femora with short stout anteroventral and posteroventral spines on at least the apical fifth. Palpus long (as in Fig. 4). Wing with cell r_{4+5} usually long petiolate (Fig. 12) .... ***Robertsonomyia*** Malloch
2 spp.: Illinois to Wyoming south to Virginia and Mexico; Camras 1944, Parsons 1948

Femora without spines ventrally. Palpus short (Fig. 2). Wing with cell r_{4+5} short petiolate or open (Fig. 13). .... ***Zodion*** Latreille
14 spp.: widespread; Camras 1943, 1944; Freeman 1968

10. Proepisternum above proepisternal bristles bare. Gena usually at least half as high as vertical diameter of eye (Fig. 4). Species usually reddish brown .... ***Myopa*** Fabricius
14 spp.: widespread; Camras 1953

Proepisternum above proepisternal bristles hairy. Gena usually less than half as high as vertical diameter of eye. Species usually black .... ***Thecophora*** Rondani
8 spp.: widespread; Camras 1945

Larva or puparium

(from Smith 1966)

1. Terminal abdominal segment with two elongate distally tapering processes projecting from posteroventral region and with tracheae extending into these structures (as in Fig. 19).. .... ***Zodion***

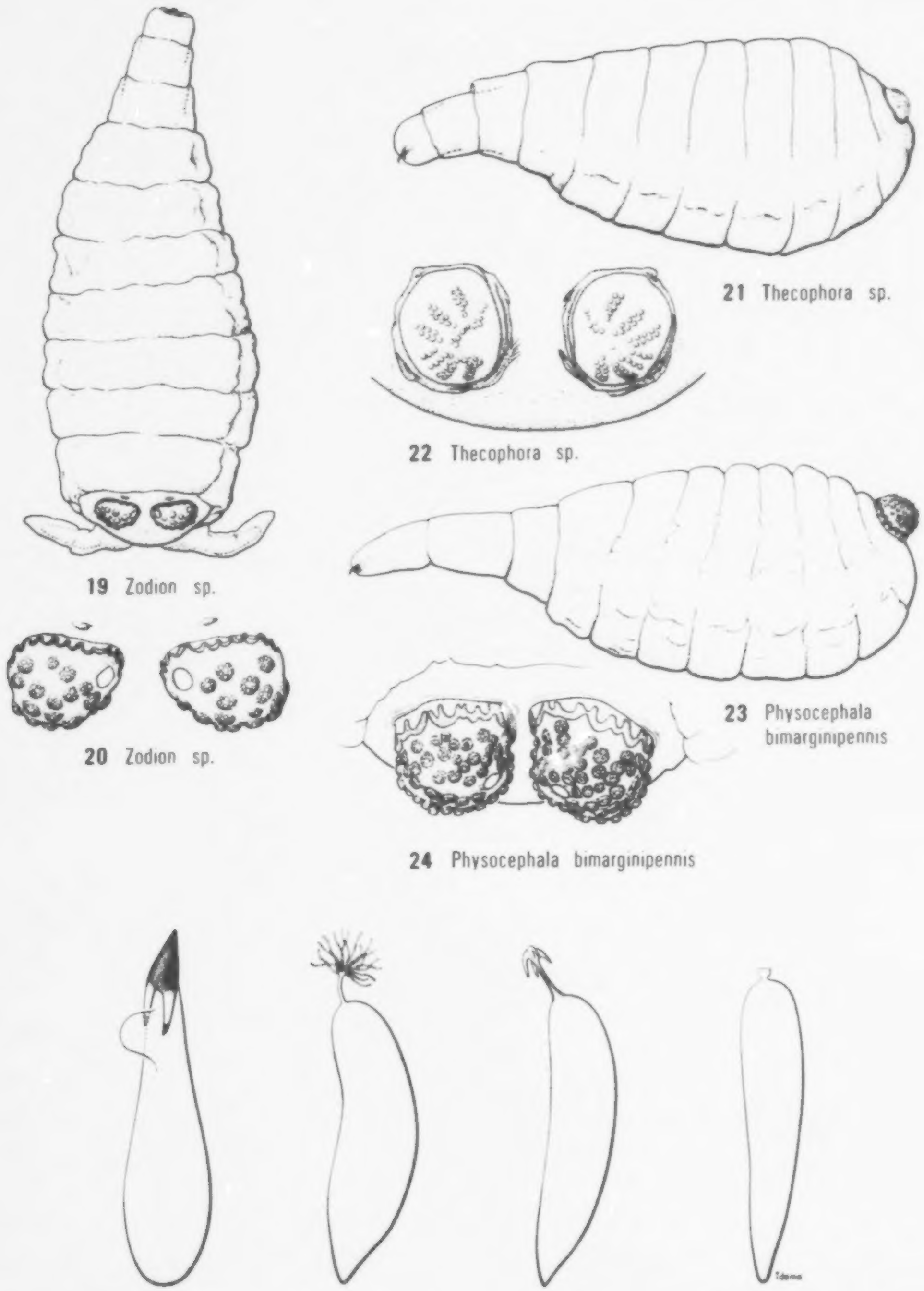
Terminal abdominal segment without such processes..............................2

2. Posterior spiracles each with 40–50 openings, confined to center, in roughly seven groups (as in Fig. 22) .... ***Thecophora***

Posterior spiracles each with wart-like protuberances over entire surface; each protuberance with numerous minute openings (as in Fig. 24) 3

3. Posterior spiracles each with 40–70 wart-like protuberances; spiracles in puparium projecting (as in Figs. 23, 24).. ***Physocephala***

Posterior spiracles with 70–110 wart-like protuberances; spiracles in puparium partly sunken, marginated, with a thin raised rim between anus and spiracles .... ***Conops***



19 Zodion sp.

20 Zodion sp.

21 Thecophora sp.

22 Thecophora sp.

23 Physocephala bimarginipennis

24 Physocephala bimarginipennis

25 Stylogaster biannulata

26 Physocephala flavipes

27 Myopa buccata

28 Dalmannia punctata

Figs. 54.19–28. Larvae, posterior larval spiracles, and eggs: (19) larva and (20) posterior larval spiracles of *Zodion* sp., dorsal view; (21) larva and (22) posterior larval spiracles of *Thecophora* sp., lateral and dorsal views, respectively; (23) larva and (24) posterior larval spiracles of *Physocephala bimarginipennis* Karsch (not Nearctic), lateral and dorsal views, respectively; eggs of (25) *Stylogaster biannulata* (Say), (26) *Physocephala flavipes* Linnaeus (not Nearctic), (27) *Myopa buccata* (Linnaeus) (not Nearctic), and (28) *Dalmannia punctata* Fabricius (not Nearctic).

Egg

1. Egg with pointed barbed head (Fig. 25) .... STYLOGASTERINAE .... *Stylogaster*
Egg with filamentous or flanged stalked micropylar processes (Figs. 26–28) 2
2. Tip of stalked micropylar process with many filamentous branches (Fig. 26) .... CONOPINAE .... *Physocephala*
Tip of stalked micropylar process simpler (Figs. 27, 28) 3
3. Micropylar process long, with four terminal hook-like flanges (Fig. 27) .... MYOPINAE .... *Myopa*
Micropylar process short, without flanged tip (Fig. 28) .... DALMANNIINAE .... *Dalmannia*

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CYPSELOSOMATIDAE

55

J. F. MCALPINE

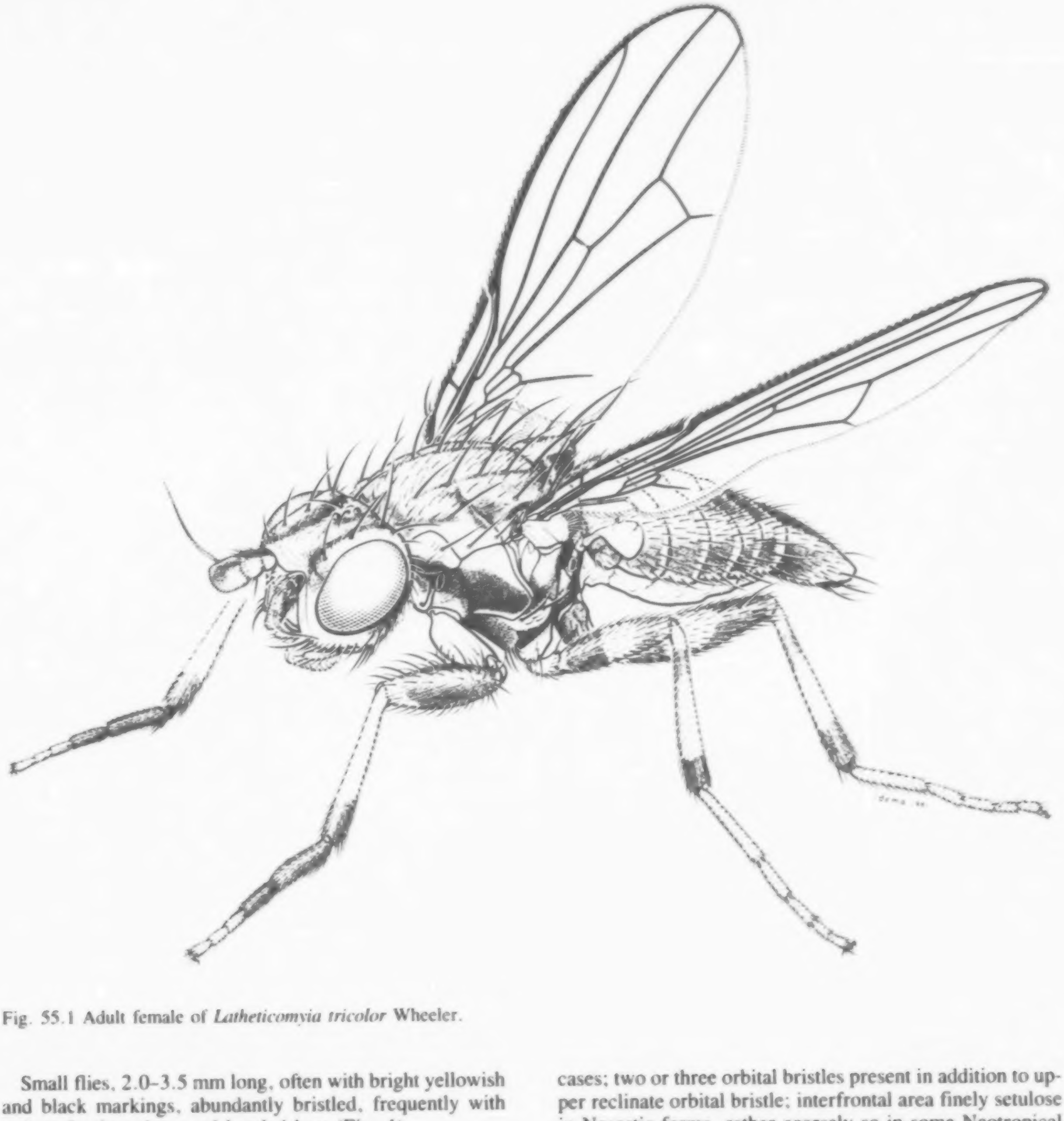


Fig. 55.1 Adult female of *Latheticomyia tricolor* Wheeler.

Small flies, 2.0–3.5 mm long, often with bright yellowish and black markings, abundantly bristled, frequently with rather slender wings and banded legs (Fig. 1).

Adult. Head: in Nearctic representatives (Fig. 2) about as long as high, but higher than long in most other genera, and about as wide as thorax. Frons usually as long from lunule to anterior ocellus as wide at latter point; orbital plate extending far forward, almost to level of lunule in some cases; two or three orbital bristles present in addition to upper reclinate orbital bristle; interfrontal area finely setulose in Nearctic forms, rather coarsely so in some Neotropical genera, e.g. *Pseudopomyzella* Hennig. Ocellar, inner and outer vertical, and postocellar bristles moderately strong; postocellar bristles slightly convergent in Nearctic forms, divergent in Cypselosomatinae; paravertical bristles present, but weak, in Nearctic species. Lunule transverse and unexposed. Face frequently rather strongly receding, usually desclerotized and sunken along midline anteriorly, bare and without carina in Nearctic forms, but carinate or tuberculate above and occasionally setulose in some extralimital genera, e.g. *Pseudopomyzella*; parafacial narrow, bare. Clypeus rather small and narrow; gena up to about one-third height of eye; vibrissa strong; a series of subvibrissal setulae and one to several stronger genal bristles present posteriorly. Compound eye nearly round or slightly horizontally oval, bare, unpatterned. Antenna short and porrect; scape very small, with a few fine setulae; pedicel somewhat elongate and swollen, weakly notched apicodorsally, with numerous fine setulae and one outstanding bristle; first flagellomere orbicular, about as long as wide, with a subapical dorsal arista; arista shortly haired. Proboscis short, with large fleshy labella; palpus club-like.

Thorax: shining blackish to dull yellow, usually with flattened disc. Prescutellum undeveloped; subscutellum weakly to moderately developed; prosternum very narrow, free from proepisternum, but continuous with mesosternal area.

Chaetotaxy: one postpronotal and one presutural supra-alar bristle present; one presutural and three or four postsutural dorsocentral bristles present; one prescutellar acrostichal bristle present or absent; one supra-alar and one or two postalar bristles present; scutellum usually with one (sometimes two) lateral bristles, one subapical marginal scutellar bristle, and additional discal setulae; one proepisternal and no proepimeral bristle present; anepisternum bare, except in Neotropical genus *Pseudopomyzella*; anepimeron bare; katepisternum usually with two bristles and additional setulae, sometimes bare; prosternum and metasternal area bare.

Wing (Fig. 3) clear to darkly fumose, often rather long and narrow in outline, but usually with strong anal angle and well-developed alula. C reaching to R_{4+5}, with costagial, humeral, and subcostal breaks; costagium with several long spines; C not spinose in Nearctic forms, but costal spines distinctly present in some extralimital genera, e.g. *Heloclusia* Malloch and *Tenuia* Malloch. Sc incomplete, fading out on apical half and more or less fused with R_1. R bare even at base; R_1 ending close to apex of Sc in basal third of wing. Crossvein between cells bm and dm strongly to very weakly developed (weak in Nearctic species); crossvein r-m joining cell dm well beyond middle of this cell; crossvein dm-cu subparallel to crossvein r-m, and less than, to more than, its own length from wing margin. CuA_1 terminating abruptly before the wing margin. Cell cu*p* present and convexly closed; A_1 usually not attaining wing margin. Upper calypter small; lower calypter scarcely developed. Halter entirely whitish.

Legs moderately strong. Fore femur with a row of posterodorsal and posteroventral bristles; mid and hind femora with a few anterior bristles near apices. Tibiae frequently banded, without preapical dorsal bristles; mid and hind tibiae with a weak apical ventral bristle in Nearctic species. Tarsi slender; front tarsi frequently mainly blackish, sometimes showing sexual dimorphism.

Abdomen: subcylindrical to moderately broad, and conspicuously setose, especially along posterior margins of the tergites. Seven spiracles present in both sexes.

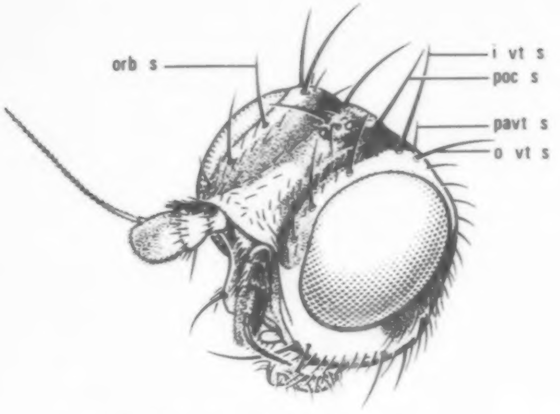
Male (Fig. 5) with segment 6 complete; sternite 6 nearly symmetric and in a ventral position. Sternite 7 mainly in a left lateral position; syntergosternite 7 + 8 distinctly shorter than epandrium, usually bristled, and usually with an outstanding pair of bristles posteriorly. Epandrium elongate, strongly flexed anteroventrally, usually with a pair of long strong bristles dorsally near base; these bristles weakly developed in Nearctic species. Surstylus simple in form, free from epandrium, and moveable. Hypandrium projecting posteroventrally from ventral wall of epandrium, forming a cone-like base for attachment of aedeagus; gonopod largely atrophied; paramere small and weakly sclerotized, usually bearing a few very tiny setulae; aedeagus with a long somewhat strap-like basiphallus and a slender more or less membranous convoluted apical section; aedeagal apodeme rod-like; ejaculatory apodeme moderately large and conspicuous in Nearctic species.

Female (Fig. 4) with segment 6 somewhat longer than preceding ones. Segment 7 with tergite and sternite at least partially fused laterally to form cone-shaped oviscape; hind margins of oviscape with two dorsal and two ventral strap-like extensions. Ovipositor mainly membranous, telescoped within segment 7; cerci small, free from each other; two small sclerotized spermathecae present in some species, not visible in others.

Biology and behavior. The immature stages are known for one Australian species, *Cypselosoma australis* D. K. McAlpine. The larva of that species was fully described by D. K. McAlpine (1966), but nothing is known about any Nearctic species.

Scarcely anything is known about the biology of the family. *Cypselosoma australis* was reared from maggots found in dung of bent-wing bats, *Miniopterus schreibersi* (Kuhl), in the Carrai bat cave near Kempsey, New South Wales (D. K. McAlpine 1966). Adults of *Polypathomyia stackelbergi* Krivosheina were reared from larvae found under bark of *Amur maackia*, amur oak, and *Aralia* sp. in Khabarovsk Territory and Kunashir Island, U.S.S.R. (Krivosheina 1979). Adults of *Latheticomyia tricolor* Wheeler and *L. lineata* Wheeler were taken in late evening at banana-baited trap-cans set out to attract Drosophilidae in Arizona and Utah (Wheeler 1956).

Classification and distribution. The family Cypselosomatidae, including the Pseudopomyzidae, is believed to be one of the most primitive groups of the Nerioidea (D. K. McAlpine 1966; Hennig 1971*a*, 1971*b*; Griffiths 1972). Its two main components, here treated as subfamilies Cypselosomatinae and Pseudopomyzinae, were treated as separate families by D. K. McAlpine (1966) and Hennig (1969, 1971*a*, 1971*b*, 1973), but Griffiths (1972) combined them into a single family. An additional synapomorphic character indicating their monophyly is the peculiar pair of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i vt s
poc s
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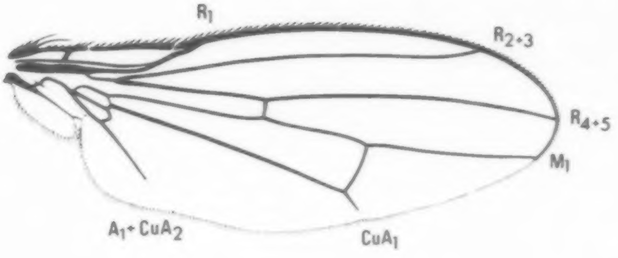
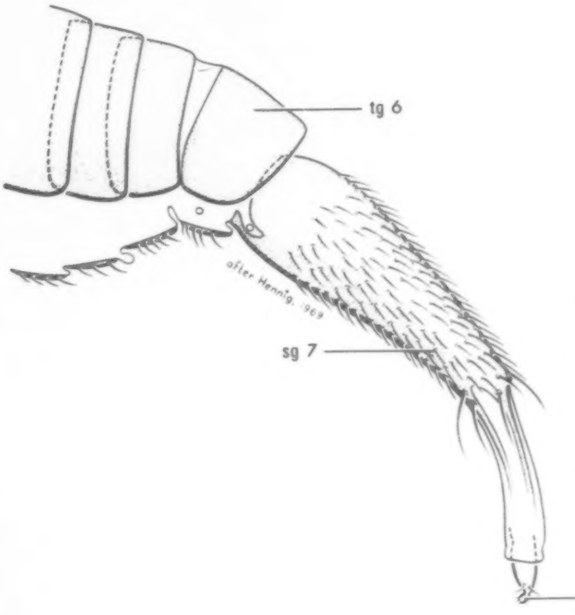
o vt s

2 Latheticomyia tricolor ♀


R_1
R_{2+3}
R_{4+5}
M_1
A_1+CuA_2
CuA_1

3 Latheticomyia tricolor ♀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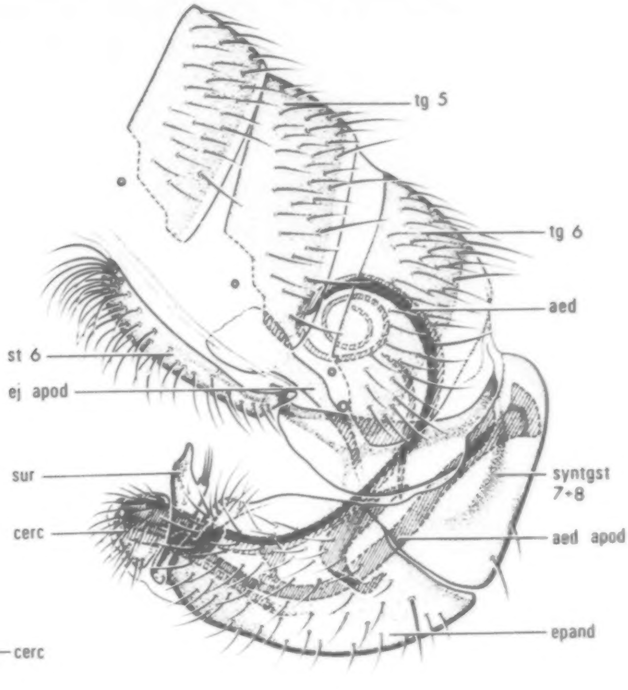
4 Latheticomyia longiterebra ♀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5 Latheticomyia tricolor ♂

Figs. 55.2-5. Head, wing, and abdomen: (2) head of *Latheticomyia tricolor* Wheeler; (3) wing of same; (4) ovipositor of *L. longiterebra* Hennig (redrawn from Hennig 1969); (5) terminalia of *L. tricolor*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pavt s, paravertical seta; poc s, postocellar seta; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

outstanding bristles on syntergosternite 7 + 8 and on the epandrium (Fig. 5). The Pseudopomyzinae is distinguished from the Cypselosomatinae by the following characters: R_{4+5} and M more or less parallel at apices (distinctly convergent in Cypselosomatinae), postocellar bristles convergent (divergent in Cypselosomatinae), paravertical bristles present though weak (absent in Cypselosomatinae), and katepisternum bristled (bare in extant Cypselosomatinae). The subfamily Cypselosomatinae contains two extant genera, *Cypselosoma* Hendel and *Formicosepsis* Meijere, both from the Indo-Australian region, and one fossil species, *Cypselosomatites succini* Hennig, from Baltic amber (Hennig 1965). The subfamily Pseudopomyzinae contains seven extant genera, as follows: *Heloclusia* Malloch (Chile), *Latheticomyia* Wheeler (northern South America, southern North America), *Polypathomyia* Krivosheina (eastern Asia), *Pseudopomyza* Strobl (Palaearctic), *Pseudopomyzella* Hennig (Peru), *Rhinopomyzella* Hennig (Ecuador, Brazil, Jamaica), and *Tenuia* Malloch (Philippine Islands); for keys see D. K. McAlpine (1966), Steyskal (1971), and Krivosheina (1979). One fossil species of Pseudopomyzinae, *Eopseudopomyza kuehnei* Hennig, is also known from Baltic amber (Hennig 1971*b*).

Only the genus *Latheticomyia* (Pseudopomyzinae) occurs in the Nearctic region, and it is so far represented here by only two species from Arizona (Wheeler 1956).

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MICROPEZIDAE

56

GEORGE C. STEYSKAL

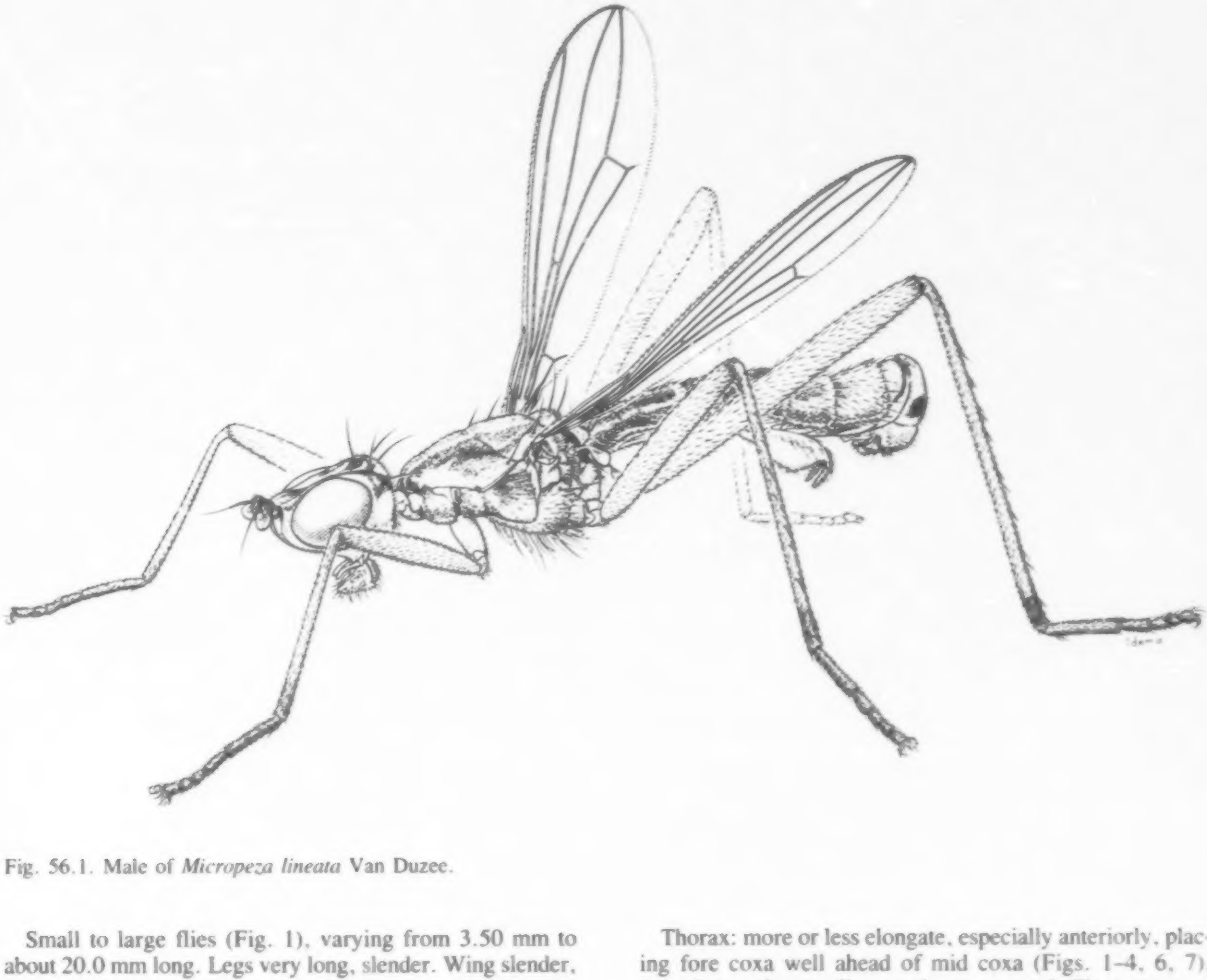


Fig. 56.1. Male of *Micropeza lineata* Van Duzee.

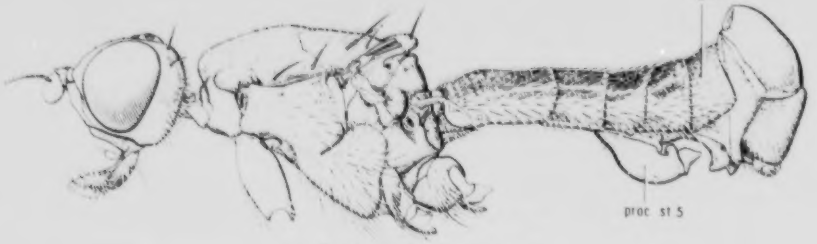
Small to large flies (Fig. 1), varying from 3.50 mm to about 20.0 mm long. Legs very long, slender. Wing slender, sometimes colorless, or yellowish or even blackish with various patterns of spots and bands of dark brown. Body color varying from yellow or reddish to brown or black, sometimes variegated with bands, and sometimes with patterns of grayish pruinescence.

Adult. Head: more or less globular in North American species (Figs. 1–4, 6, 7), often conical and bluntly extended behind eyes and pointed forward in Micropezinae (Fig. 1). Eye well-developed. Antenna of moderate size, with bare or haired subbasal arista. Proboscis rather robust, never elongated or otherwise specialized. Chaetotaxy: no vibrissae or ocellar bristles; inner and outer vertical bristles and one upper fronto-orbital bristle nearly always present; zero or one postocellar bristle and zero to two erect or recurved lower fronto-orbital bristles present.

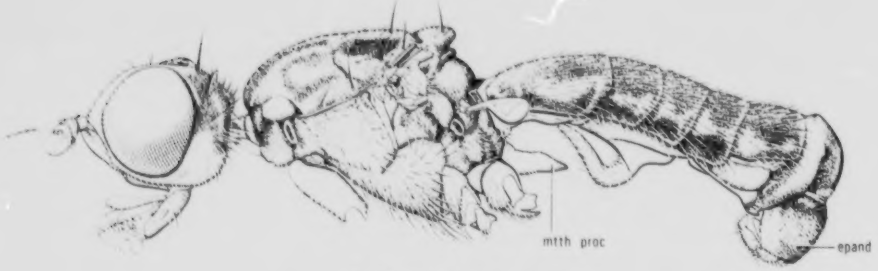
Thorax: more or less elongate, especially anteriorly, placing fore coxa well ahead of mid coxa (Figs. 1–4, 6, 7). Scutellum rather small, sometimes upturned. Chaetotaxy: no postpronotal, proepisternal, or anepisternal bristles; katepisternum with several to many bristles posteriorly; scutum with zero to four dorsocentral bristles, one supra-alar and one postalar bristle, one or two notopleural bristles, and two (one pair) scutellar bristles.

Legs long and slender (Fig. 1). Preapical tibial bristles lacking, but in Calobatinae a series of rather short more or less uniform dorsal setae present. In a few Taeniapterinae, femora, especially hind femur, club-like with preapical swelling, without ventral bristles.

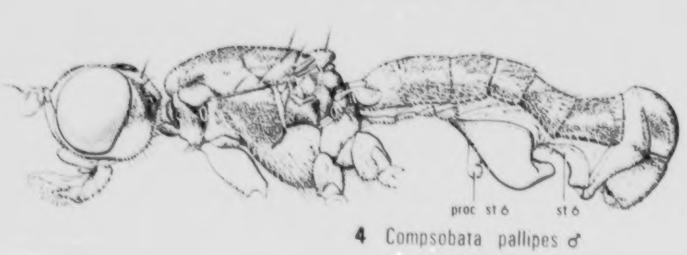
Wing long and slender (Figs. 9–13). C reaching M_{1+2} without costal breaks; Sc complete and free or occasionally closely adjacent to R_1 near apex (Fig. 10); all longitudinal veins more or less straight and extending to wing margin;



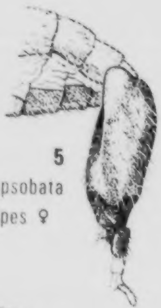
2 Compsobata univitta ♂



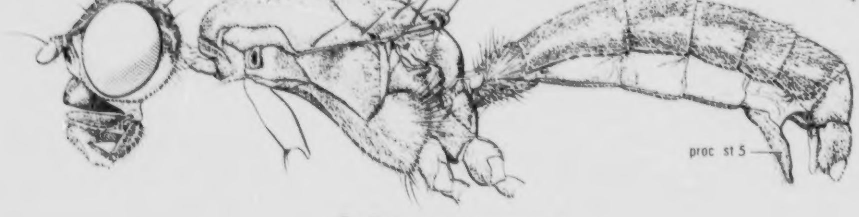
3 Cnodacophora nasoni ♂



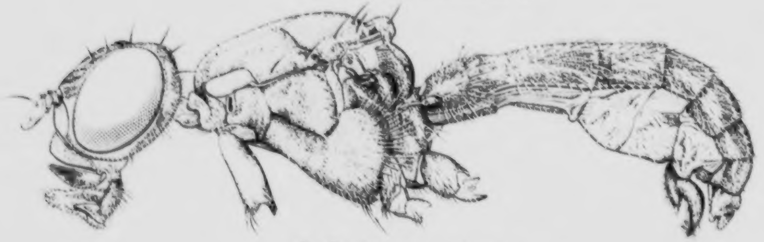
4 Compsobata pallipes ♂



5 Compsobata pallipes ♀



6 Rainieria antennaepes ♂



7 Taeniaptera trivittata ♂

Figs. 56.2–7. Lateral views: bodies of male of (2) *Compsobata univitta* (Walker), (3) *Cnodacophora nasoni* (Cresson), and (4) *Compsobata pallipes* (Say); (5) posterior segments of abdomen of female of *Compsobata pallipes*; bodies of male of (6) *Rainieria antennaepes* (Say) and (7) *Taeniaptera trivittata* Macquart.

Abbreviations: epand, epandrium; mtth proc, process of metathorax; proc st, process of sternite; st, sternite.

R_{4+5} and M_{1+2} usually convergent or fusing at or near wing tip; CuA_2 closing cell cu*p* straight (Figs. 9–11) and sometimes quite oblique (Fig. 12); $A_1 + CuA_2$ usually rather short, sometimes reaching wing margin. Wing pattern, when present (Figs. 12, 13), consisting of bands or a few spots, or both.

Abdomen: more or less elongate (Figs. 1–4, 6, 7), sometimes petiolate, with seven spiracles in both sexes. Terminalia of both sexes flexed downward or downward and forward.

Female with tergite and sternite of segment 7 fused ventrolaterally, but usually with traces of lines of fusion, and bearing seventh pair of spiracles at base ventrally; segment 7 heavily sclerotized, variously elongate, sometimes somewhat compressed laterally or variously expanded basally, housing membranous ovipositor (Fig. 5). Two or three small sclerotized spermathecae present; cerci free, but small.

Male frequently with specialized forceps-like processes of variable size, shape, and ornamentation arising from sternite 5; sternite 6 sometimes with specialized processes (Figs. 2–4, 6–8), occasionally with a specialized process on metathorax situated between hind coxae (Fig. 3). Tergite and sternite of segment 7 at least partially fused, somewhat reduced, and displaced laterally on left side; occasionally small remnants present on right side also; spiracle 7 of left side situated at anterior margin or in tergal portion of this syntergosternite and spiracle 7 of right side in membrane or in isolated remnant of this sclerite. Syntergosternite 8 well-developed but not enlarged, occasionally with a faint incomplete suture present dorsolaterally on right side. Epandrium well-developed; its hind margin straight or variously notched medially; posteroventral corners sometimes slightly produced under cerci. Surstyli present and well-developed or absent; sternite 10 plate-like, usually moderately large; cerci free, small to moderately large. Hypandrium moderately large, U-shaped, with a strong hypandrial bridge and a short and broadly rounded to long and slender hypandrial apodeme; aedeagal guide well-developed; gonopods present but variable in size; parameres well-developed, rod- or plate-like, but variable in size; aedeagus long and slender, often with sclerotized rods or plates; aedeagus unjointed or with a sclerotized bulbous joint near middle; aedeagal apodeme variable in size but usually long. Sperm pump and ejaculatory duct strongly developed.

Egg. Recorded for only one species, presumably *Micropeza corrigiolata* Linnaeus (Müller 1957). About 0.9 mm long, with a finely areolate chorion, found in earth.

Larva. Typically maggot-shaped, with a mostly smooth cuticle (Fig. 14). Mandible simple, claw-like, without teeth, and not accompanied by accessory oral sclerites (Figs. 15, 17, 18). Anterior spiracles (Fig. 14) more or less fan-shaped, placed laterally. Posterior spiracles (Fig. 16) separated, each with at least one dorsal respiratory spine; posterior spiracular openings consisting of three or four slits or numerous pores; spiracular hairs of posterior spiracles in four small tufts on roundish bases.

Larvae of only a few species are described (Wallace 1969, Teskey 1972). The four known North American larvae can be distinguished as indicated in the larval key.

Puparium. As in most muscoids, formed from hardened last larval skin, and therefore presenting most characters of mature larva.

Biology and behavior. Although most of the species of Micropezidae that have been reared were from decaying vegetable matter and dung, one species is known to attack live ginger roots in the Orient (Steyskal 1964), and a species of *Micropeza* Meigen has been found in Europe devouring the contents of root nodules of leguminous plants (Müller 1957). A more complete account of the biology and behavior of the Micropezidae can be found in Merritt and James (1973).

Classification and distribution. Because of their long legs, the Micropezidae are often called stilt flies, and earlier literature treats them under various family names, including Calobatidae, Taeniapteridae, Trepidariidae, and Tylidae. About 500 world species are known and most of these are found in the tropics with only 27 recorded from the United States and Canada.

The monograph of the world species of Micropezidae by Hennig (1934, 1935*a*, 1935*b*, 1936) is very useful. For North America, Cresson (1938) is indispensable. Papers by Merritt (1970, 1971, 1972), Merritt and James (1973), and Merritt and Peterson (1976) are also important. Hennig (1973) divided the group into three distinct families, the Micropezidae, the Calobatidae, and the Taeniapteridae, but the more traditional views of recognizing a single family (Griffiths 1972, McAlpine 1974) are followed here.

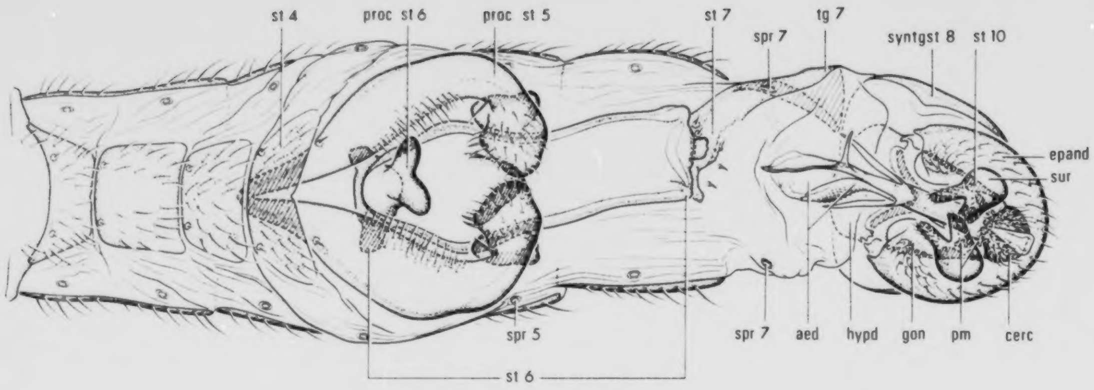
Bachofen-Echt (1949) mentioned that three species of *Calobata* Meigen were known from Baltic amber, but Hennig (1965) only lists two species, both in the genus *Electrobata* Hennig.

Keys to genera

Adult

1. Hind tibia with a row of dorsal bristles (Fig. 1). Crossvein bm-cu present or absent. Katepisternal bristles present and often numerous 2

Hind tibia without a row of dorsal bristles. Crossvein bm-cu present, separating cells bm and dm (Figs. 9, 10). One to four katepisternal bristles present .....CALOBATINAE....4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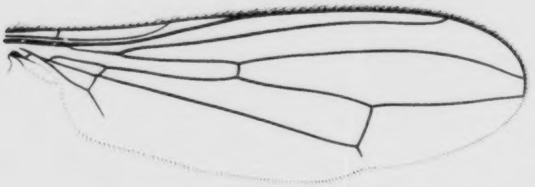
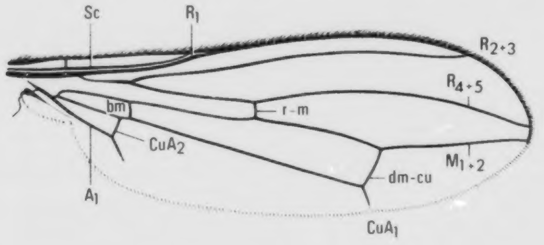
8 Compsobata mima ♂



9 Cnodacophora nasoni ♀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dm-cu
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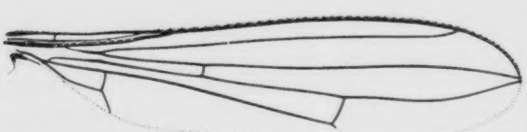
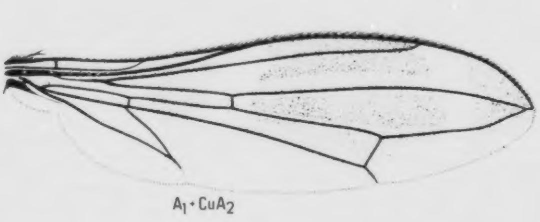
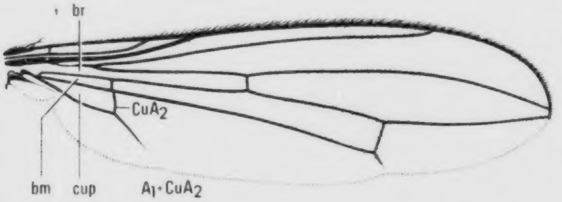
10 Compsobata mima ♀



11 Micropeza lineata ♀



12 Taeniaptera trivittata ♂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CuA_2
bm
cup
A_1+CuA_2

13 Rainieria antennaepes ♂

Figs. 56.8–13. Male abdomen and wings: (8) abdomen in ventral view of male *Compsobata mima* (Hennig); wings of (9) *Cnodacophora nasoni* (Cresson), (10) *Compsobata mima*, (11) *Micropeza lineata* Van Duzee, (12) *Taeniaptera trivittata* Macquart, and (13) *Rainieria antennaepes* (Say).

Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; proc st, process of sternite; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

2. Crossvein bm-cu absent and cells bm and dm confluent; posterodistal angle of cell cu*p* not acute (Fig. 11). Fronto-orbital bristles absent (Fig. 1). One to four katepisternal bristles present .... MICROPEZINAE .... ***Micropeza*** Meigen 3

Cresson 1938; Hennig 1934, 1935*a*, 1935*b*, 1936; Merritt and James 1973

Crossvein bm-cu present and cells bm and dm separate; posterodistal angle of cell cu*p* acute (Figs. 12, 13). Fronto-orbital bristles present (Figs. 6, 7). Katepisternal bristles numerous in vertical series .... TAENIAPTERINAE 6

3. One notopleural bristle present (Fig. 1). Cell r_{4+5} open or closed in margin (Fig. 3) .... ***Micropeza*** (***Micropeza*** Meigen)

10 spp.; northern Great Plains southward into Neotropical region

Two notopleural bristles present. Cell r_{4+5} usually closed and often petiolate .... ***Micropeza*** (***Neriocephalus*** Enderlein)

6 spp.; northern Great Plains southward into Neotropical region

4. Palpus more than twice as long as wide, reaching facial margin (Fig. 3). Subcostal section of C long (Fig. 9). Male with metathoracic process situated between bases of hind coxae (Fig. 3) .... ***Cnodacophora*** Czerny

3 spp.; northward from Colorado and Illinois

Palpus little longer than broad, not reaching facial margin (Fig. 2). Subcostal section of C virtually obliterated by Sc and R_1 lying adjacent at tips (Fig. 10). Male without metathoracic process (Fig. 2) .... ***Compsobata*** Czerny 5

5. Sternite 6 of male without a process projecting between bases of processes of sternite 5. Female with segment 7 laterally compressed, rounded basally. Body color reddish; thorax wholly pruinose dorsally .... ***Compsobata*** (***Compsobata*** Czerny)

2 spp.; widespread, mostly northward

Sternite 6 of male with at least a small process projecting between bases of processes of sternite 5 (Figs. 4, 8). Segment 7 of female sometimes with an ear-like lobe basally (Fig. 5) and cylindrical or flattened dorsoventrally. Body color black; thorax partly glossy dorsally .... ***Compsobata*** (***Trilophyrobata*** Hennig)

13 spp.; widespread, mostly northward

6. Anterior margin of clypeus with a few short erect setae. Arista bare. Postocellar bristles lacking .... ***Hoplocheiloma*** Cresson

1 sp., *fabricii* Steyskal; Florida (second species Neotropical)

Clypeus bare. Other characters variable 7

7. Median part of face broad, flattened, and setose .... ***Calobatina*** Enderlein

1 sp., *geometra* (Robineau-Desvoidy); southeastern U.S.A. to Pennsylvania and Texas; Steyskal 1971

Median part of face narrow and bare 8

8. Cell cu*p* long; CuA_2 as long as or longer than free part of $A_1 + CuA_2$ (Fig. 12) .... ***Taeniaptera*** Macquart

2 spp.; north to California, Michigan, and New York (other species Neotropical); Cresson 1938

Cell cu*p* short; CuA_2 shorter than free part of $A_1 + CuA_2$ (Fig. 13) 9

9. Arista plumose (shortly so in Nearctic species). Pruinose frontal vitta broad at each end .... ***Grallipeza*** Rondani

1 sp., *nebulosa* (Loew); Gulf States; Cresson 1938

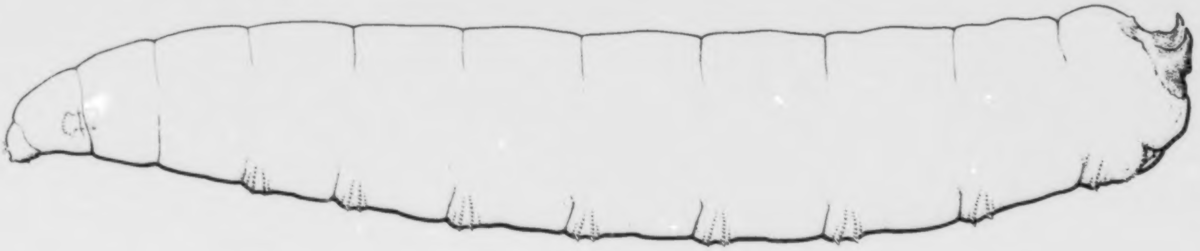
Arista bare (plumose in some extralimital species). Pruinose frontal vitta strongly narrowed anteriorly .... ***Rainieria*** Rondani

1 sp., *antennaepes* (Say); Alberta and Nova Scotia south to Texas and Florida (other species Neotropical)

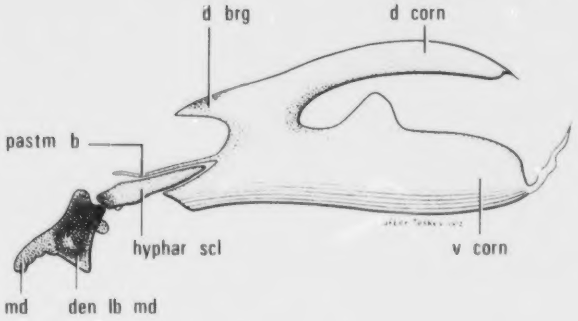
Larva

1. Posterior spiracle bearing a dorsal respiratory spine as long as diameter of base; spiracular openings in four vertical slits; two fan-like tufts of spiracular hairs borne on base of respiratory spine (Fig. 16). Anterior spiracle with seven or eight papillae .... ***Compsobata univitta*** (Walker)

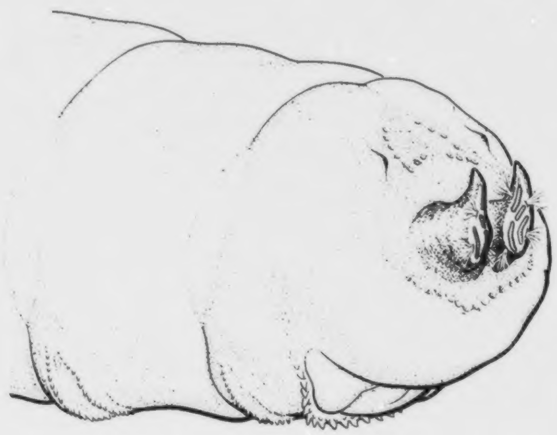
Posterior spiracle with much shorter respiratory spine. Anterior spiracle with about 15 papillae 2



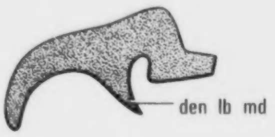
14 Compsobata univitta



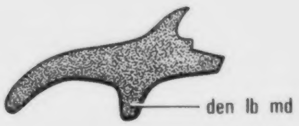
15 Compsobata univitta



16 Compsobata univitta



17 Rainieria antennaepes



18 Taeniaptera lasciva

Figs. 56.14–18. Larva and larval structures: (8) larva of *Compsobata univitta* (Walker); (15) cephalopharyngeal skeleton of *Compsobata univitta*; (16) posterior segments of larva of *Compsobata univitta*; mandibles of (17) *Rainieria antennaepes* (Say) and (18) *Taeniaptera lasciva* (Fabricius).

Abbreviations: d brg, dorsal bridge; d corn, dorsal cornu; den lb md, dental lobe of mandible; hyphar scl, hypopharyngeal sclerite; md, mandible; pastm b, parastomal bar; v corn, ventral cornu.

2. Openings of posterior spiracle consisting of 40 or more irregularly disposed oval pores. Ventral cornu of cephalopharyngeal skeleton with a dorsal lobe situated at anterior third of its length .... ***Calobatina geometra*** (Robineau-Desvoidy)

Openings of posterior spiracle otherwise. Dorsal lobe of ventral cornu situated close to stem of dorsal cornu 3

3. Posterior spiracle with numerous openings arranged in irregularly serpentine series. Dental lobe of mandible curved basally (Fig. 17) .... ***Rainieria antennaepes*** (Say)

Posterior spiracle with three oval or sausage-shaped openings. Dental lobe of mandible perpendicular (Fig. 18) .... ***Taeniaptera lasciva*** (Fabricius)

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NERIIDAE

57

George C. Steyskal

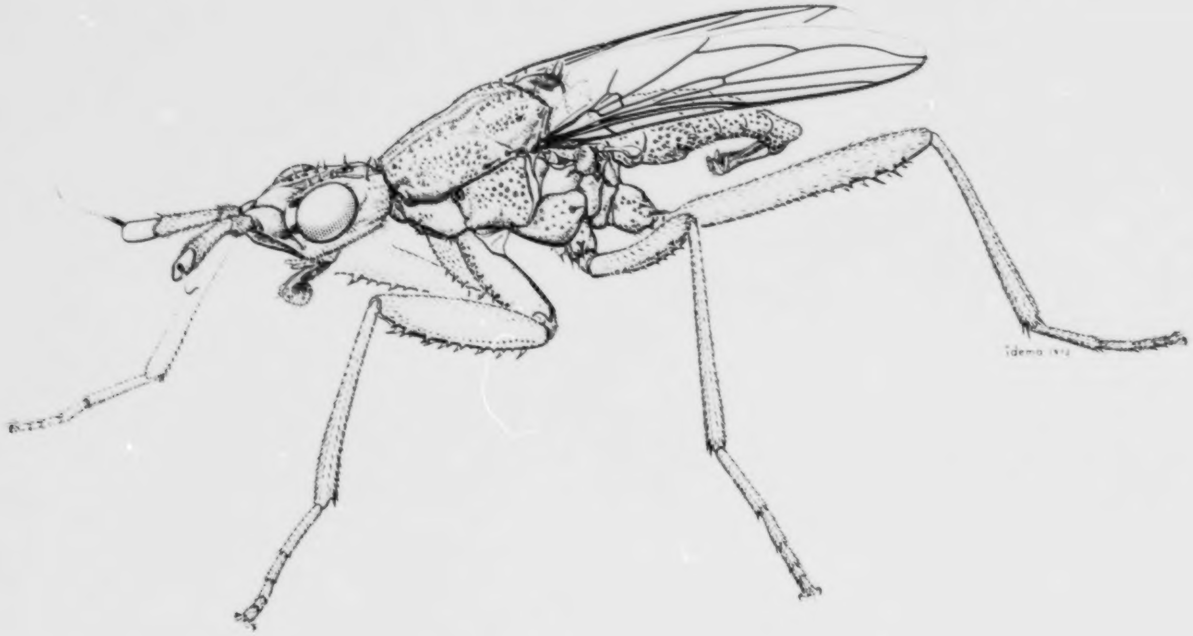

Fig. 57.1. Male of *Odontoloxozus longicornis* (Coquillett).

Slender brown to blackish flies (Fig. 1), sometimes variegated with shades of yellow or orange, rather dull, often with a pruinose scutal pattern. Wing hyaline, yellowish or brownish, without a sharply defined color pattern. Bristles usually reduced in number and length, but often rather stout and placed on wart-like bases. Length 7.0–12.0 mm in Nearctic species.

Adult. Head: longer than high (Figs. 1–3), with occipital area well-developed. Bristles short; postocellar bristles convergent; short stout genal bristle usually present; vibrissae absent in Nearctic species. Antenna porrect, of moderate size to rather elongate; pedicel with a process lying against medial side of first flagellomere; first flagellomere conical to rectangular in shape; arista dorsally subapical to apical, bare or with dense short hairs. Palpus and proboscis well-developed, but short and retractable into oral cavity.

Thorax: much higher and longer than wide (Fig. 1). Scutellum bare, with a single pair of apical bristles which are usually the longest and strongest of thoracic bristles; one katepisternal bristle usually evident. Greater ampulla moderately well-developed. Wing (Fig. 4) shorter than body, narrow; Sc complete, ending in a weakened or interrupted place in C; C otherwise uninterrupted, ending in M_{1+2}; cell cu*p* small; CuA_2 more or less retrorse; free part of A_1 + CuA_2 terminating approximately halfway to wing margin. Upper calypter much larger than lower one. Legs elongate (Fig. 1), slender; fore coxa elongate; lower side of femora usually with rows of stout spinules on conical protuberances; middle femur concave dorsally.

Abdomen: elongate, with six anterior segments complete; sternites reduced to narrow longitudinal bars. Terminalia of male (Fig. 6) flexed downward and forward under anterior segments; epandrium long and cylindrical or narrowed medially; surstylus small and clavate; cercus short; aedeagus long and slender with anteriorly grooved basiphallus against which more slender distiphallus folds in repose. Female with tergite 7 and sternite 7 fused laterally and bearing seventh pair of spiracles at base ventrally; ovipositor unsclerotized (Fig. 5) and retracted within segment 7 when in repose; two pairs of colorless spermathecae present.

Egg. White, elongate ellipsoidal, about 0.17–0.20 mm long and 0.89–1.09 mm wide, and with a long slender anterior filament measuring about 2.5–3.7 mm long and 0.02 mm wide. Chorion bearing longitudinal sculpture on anterior fifth and fine reticulation on remainder.

Larva. Slender, roundly tapering anteriorly, and roundly truncate posteriorly. Mandible simple, not strongly curved. Cuticle smooth; only ventral creeping welts bearing spicules. Anterior spiracles with 17–19 papillae in three groups in a transverse sinuate row; posterior spiracles on closely adjacent plates on a low rounded protuberance, with four spiracular openings on each plate arranged end-to-end in form of a C with open part of C directed medially.

The immature stages of *Odontoloxozus longicornis* (Coquillett) of North America (Olsen and Ryckman 1963, Steyskal 1965) and *Telostylinus lineolatus* (Wiedemann) of the Australasian region (Berg 1947) are the only ones previously described. *Odontoloxozus longicornis* is described above, but the other species is generally similar.

Puparium. Reddish, elongate fusiform, transversely striate. Anterior spiracles not conspicuous; posterior spiracles on truncate conical protuberances.

Biology and behavior. Larvae of *Odontoloxozus longicornis* have been reared from eggs deposited in necrotic tissue of various species of cacti and from rotten stems of *Carica papaya* L. (papaya). The Australasian species, *Telostylinus lineolatus*, was reared from sap running from wounds in papaya trees, and other species have been reared from rotting flesh of other plants.

Classification and distribution. The family is almost wholly circumtropical. Approximately 110 species are known; two-thirds of these are New World, including two that extend into southwestern United States. The American species were monographed by Aczél (1961) and cataloged by Steyskal (1968). Two subfamilies are recognized, Telostylinae and Neriinae. Only the Neriinae are American; they are distinguished by the expanded, biconvex dorsal margin of the face, which is formed into prominently exposed antennal sockets.

Key to genera

Adult

1. Anterior notopleural bristle strong; one or two postpronotal bristles present. Arista clearly dorsal, situated at anterodorsal corner of segment (Fig. 3) .... **Odontoloxozus** Enderlein

1 sp., *longicornis* (Coquillett); southwestern U.S.A.

Anterior notopleural bristle absent or much weaker than posterior bristle; postpronotal bristles absent (Fig. 1). Arista clearly apical (Fig. 2), situated near middle of anterior margin of segment .... **Glyphidops** Enderlein

1 sp., *flavifrons* (Bigot); southwestern U.S.A.

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Figs. 57.2–6. Heads, wing, and abdomens: left lateral views of head of (2) *Glyphidops flavifrons* (Bigot) and (3) *Odontoloxozus longicornis* (Coquillett); (4) wing of *Odontoloxozus longicornis;* left lateral views of terminalia of (5) female of *Odontoloxozus longicornis* and (6) male of *Glyphidops flavifrons.*

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; spm pmp, sperm pump; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

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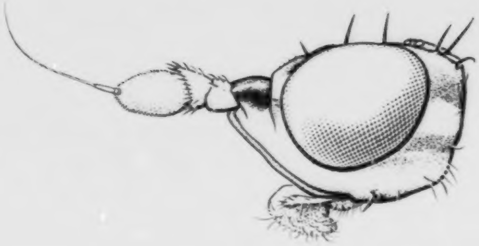
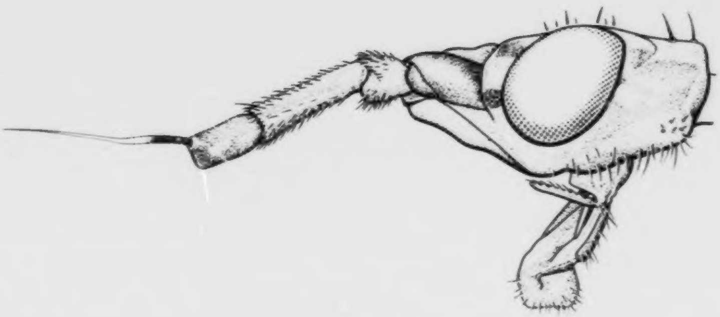
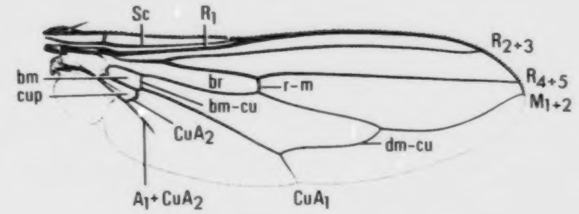


2 Glyphidops flavifrons ♂



3 Odontoloxozus longicornis ♀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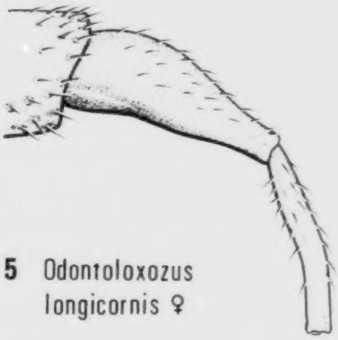
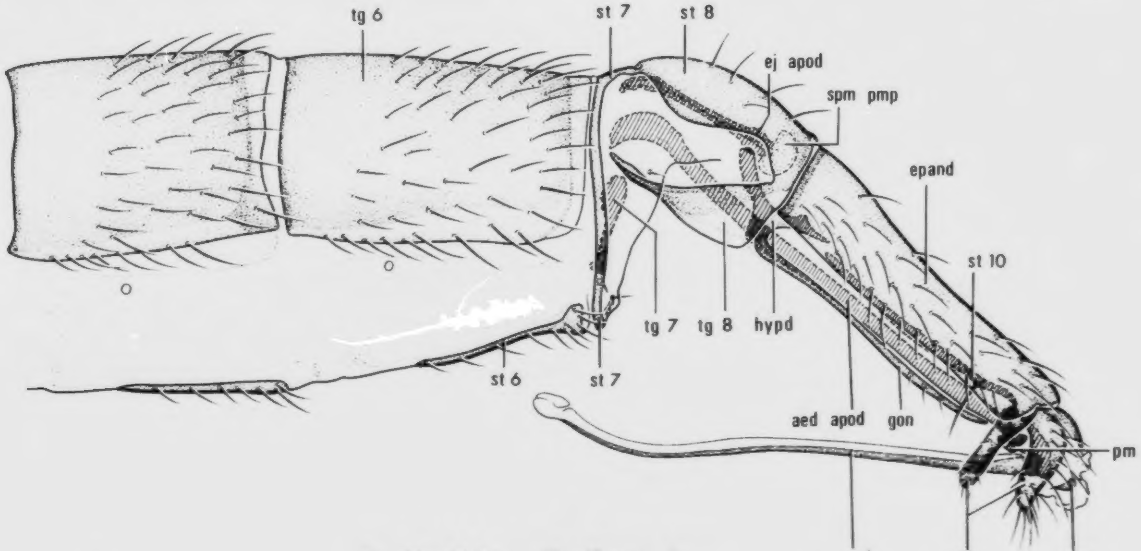
4 Odontoloxozus longicornis ♂



5 Odontoloxozus longicornis ♀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6 Glyphidops flavifrons ♂

TANYPEZIDAE

58

GEORGE C. STEYSKAL

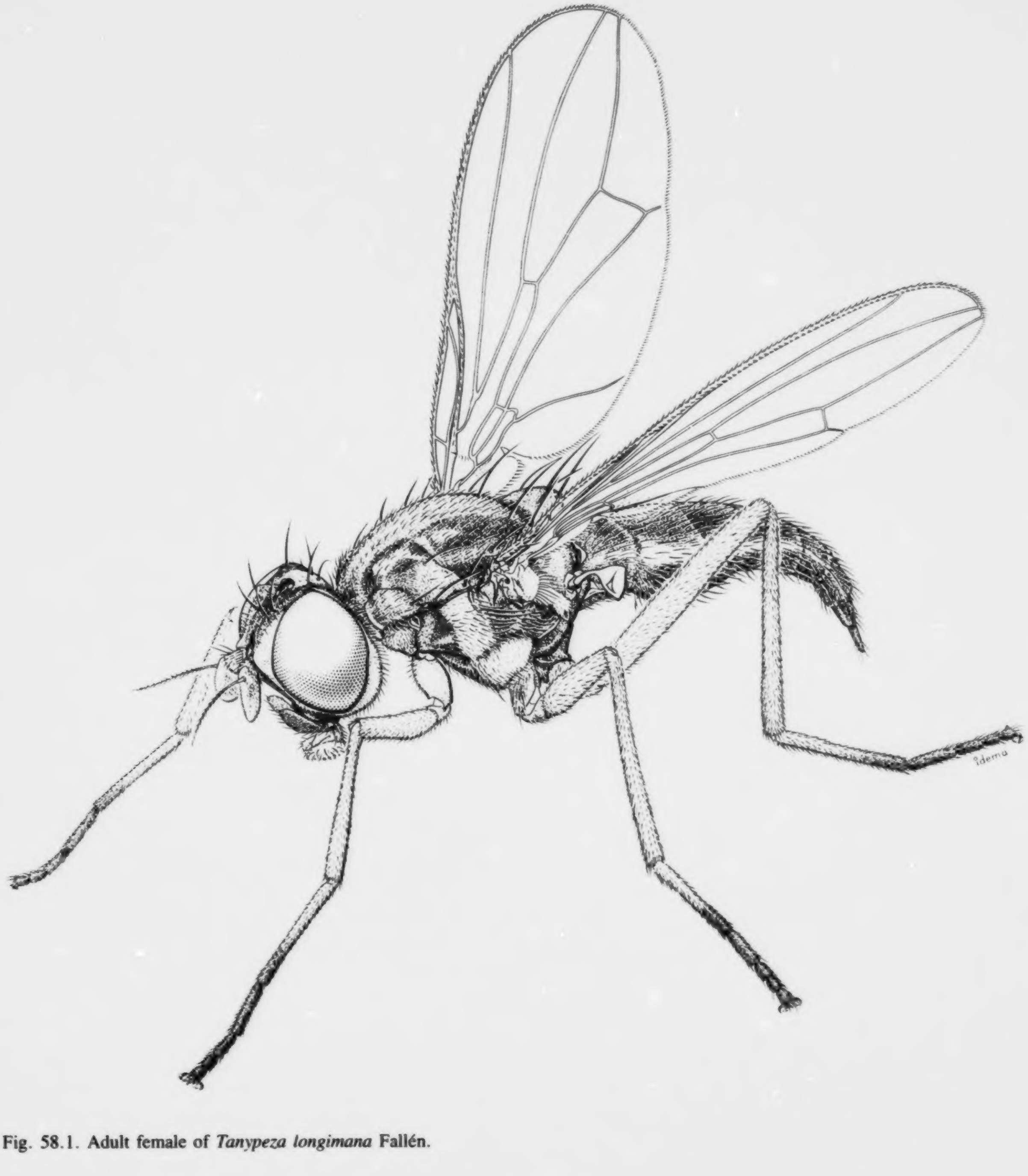


Fig. 58.1. Adult female of *Tanypeza longimana* Fallén.

North American species medium-sized flies, about 5-7 mm long (Fig. 1), with patches of silvery tomentum, and with legs and sometimes first flagellomere yellowish.

Adult. Head: hemispherical (Fig. 1). Eye very large. Frons considerably narrower than eye, and in male considerably narrower than in female; parafacial silvery, extending for some distance above antenna. Gena narrow; postgena (lower posterior orbit) a little swollen in lateral view. Occiput slightly concave. Antenna of moderate length; scape and pedicel quite small; arista subbasal, pubescent. Proboscis small; palpus elongate oval, of moderate size. Chaetotaxy: vibrissae absent; usually one weak inner and one weak outer vertical bristle present on posterior aspect of vertex; one to three orbital bristles present, one near vertex and two anterior to ocellar triangle; one pair of ocellar bristles and one pair of divergent postocellar bristles present (Fig. 1).

Thorax: stout, somewhat longer than wide. Precoxal bridge present. Chaetotaxy: pleuron setulose, with a few upper anepisternal bristles; dorsum of thorax with one postpronotal bristle, zero or one small presutural intra-alar bristle, two notopleural bristles, and one supra-alar and two postalar bristles; scutellum with two pairs of bristles present, otherwise bare (Fig. 1). Legs slender, without setae; only mid tibia with small apical hairs; male of *Tanypeza* Fallén with a few short black setae on lower side of hind trochanter and with a short row of similar setae close to base on posterior side of hind femur (Fig. 2). Wing (Fig. 1) hyaline; C with a weak subcostal break; Sc complete, meeting C at some distance before end of R_1; R_{4+5} and M approaching each other closely at tip of wing; cell cu*p* rather long, closed by reversed L-shaped CuA_2, vertical leg of which is as long as longitudinal leg; A_1 not quite attaining wing margin. Upper lobe of calypter with a series of unusually long ciliae. Halter pale, with whitish knob.

Abdomen: ovoid, with long setae laterally, especially toward base (Figs. 4, 7). Male terminalia (Figs. 6, 7) similar in many respects to that of Strongylophthalmyiidae, but sternite 6 separated from syntergosternite 7 + 8, although somewhat distorted; gonopod and paramere greatly reduced; aedeagus not obviously divided into basiphallus and distiphallus. Female terminalia (Figs. 4, 5) not adapted for piercing; segment 7 reduced to four sclerotized longitudinal strips; ovipositor elongate; cerci virtually fused; one ventral receptacle and two sclerotized spermathecae present.

Larva. Anterior spiracles biramous; each branch with eight or nine papillae. Posterior spiracles in three elliptic slits; slits disposed in T-formation in each of a pair of heavily sclerotized medially constricted sleeve-like spiracular plates at ends of small protrusions.

Detailed descriptions and illustrations for *Tanypeza longimana* Fallén were provided by Foote (1970).

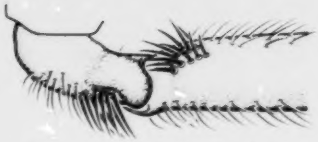
Biology and behavior. All that is known concerning the immature stages and life habits of the Tanypezidae is contained in the detailed description by Foote (1970) of larvae reared in the laboratory on decaying watermelon rind. The eggs were obtained from a female swept from a colony of yellow skunk cabbage, *Lysichiton americanum*.

Classification and distribution. The Tanypezidae are primarily a New World group, consisting of two Nearctic species of *Tanypeza*, one of which is Holarctic, and a score of Neotropical species in the genera *Scipopeza* Enderlein and *Neotanypeza* Hendel. Some members of *Neotanypeza* occur in Mexico and possibly extend marginally into the Nearctic region. The latest revision of the family is by Enderlein (1936). The two Nearctic species were distinguished by Steyskal (1965). Two publications by Hennig (1936, 1937) are also important. Griffiths (1972) included the Strongylophthalmyiidae with the Tanypezidae, but it seems best to consider the two groups as separate, although closely related, families. The Tanypezidae differ from the Strongylophthalmyiidae (and vice versa) in many features, including plesiomorphic (P), apomorphic (A), and autapomorphic conditions (AA), as follows: frons narrower in male than in female (P) (of equal width in both sexes in Strongylophthalmyiidae (A)); upper orbital bristle arising on vertex (AA) (arising in usual forward position in Strongylophthalmyiidae (P)); first flagellomere elongate (A) (short in Strongylophthalmyiidae (P)); C with a very weak subcostal break (P) (with very strong subcostal break in Strongylophthalmyiidae (A)); Sc complete (P) (incomplete in Strongylophthalmyiidae (A)); R_{4+5} and M strongly convergent (A) (not convergent in Strongylophthalmyiidae (P)); CuA_2 strongly recurved (AA) (not strongly recurved in Strongylophthalmyiidae (P)); female with two sclerotized spermathecae (P) (with one in Strongylophthalmyiidae (AA)); female abdominal segment 7 reduced to four narrow strips (AA) (wholly sclerotized tube in Strongylophthalmyiidae (P)); and male with greatly reduced paramere (AA) (well-developed in Strongylophthalmyiidae (P)). The following key includes all known genera; a few subgenera of *Neotanypeza*, distinguished only on numbers of certain setae, are not included. No fossils are known.

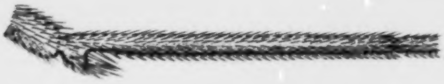
Figs. 58.2-7. Characters of legs and abdomen: (2) right hind trochanter and base of femur of *Tanypeza longimana* Fallén, posteroventral view; (3) tarsomere 1 of left hind tarsus of *Neotanypeza elegans* (Wiedemann), posterior view; (4) female abdomen and terminalia of *Tanypeza longimana*, left lateral view; (5) details of apical portion of ovipositor of *T. longimana*, ventral view; (6) details of male terminalia of *T. longimana*, ventral view; (7) male abdomen and terminalia of *T. longimana*, left lateral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; pm, paramere; sg, segment; spmth, spermatheca; syntgst, syntergosternite; tg, tergite; v rep, ventral receptacle.

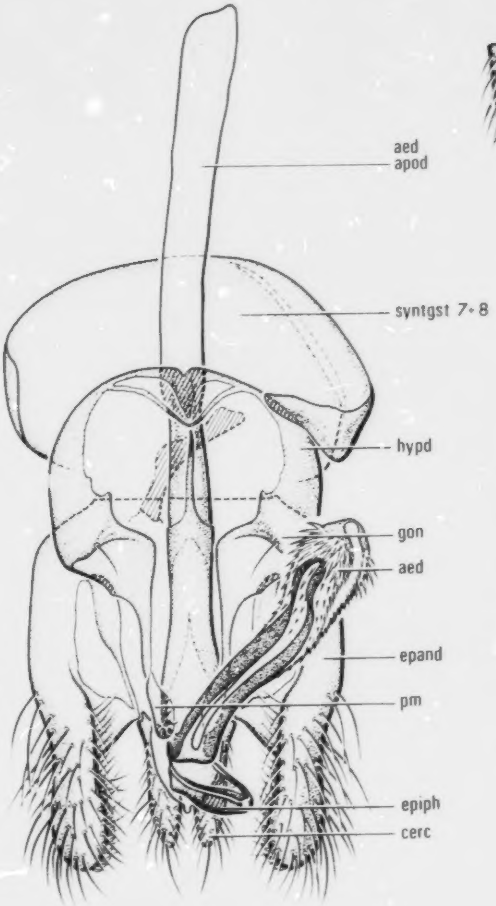
⇨



2 Tanypeza longimana ♂



3 Neotanypeza elegans ♂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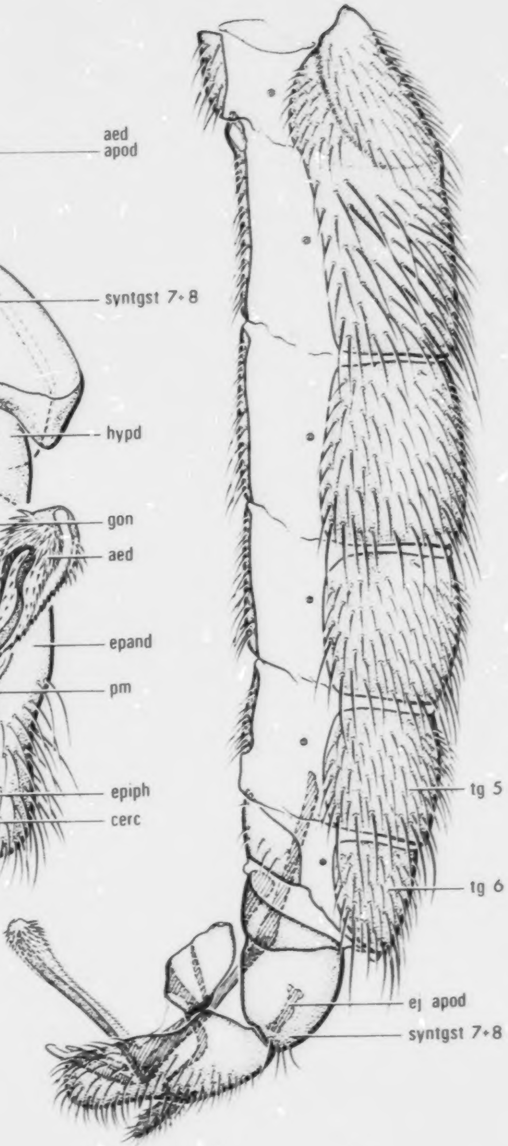
6 Tanypeza longimana ♂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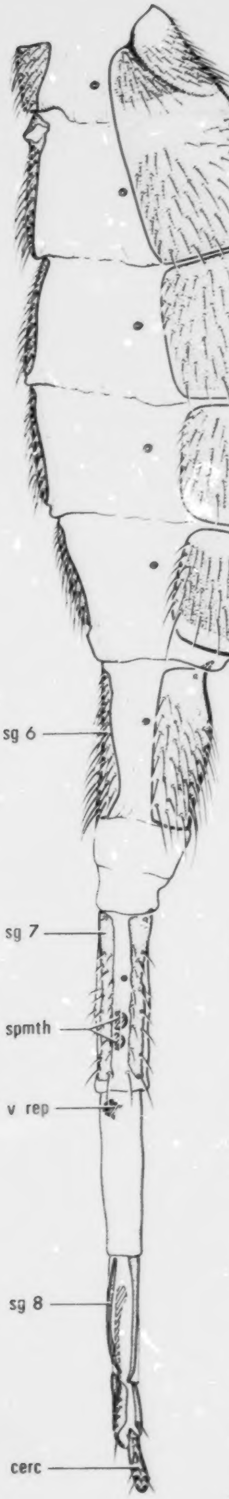
7 Tanypeza longimana ♂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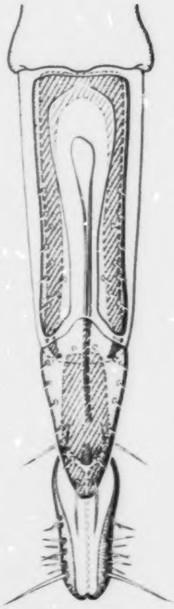
4 Tanypeza longimana ♀



5 Tanypeza longimana ♀

Key to genera

1. Base of tarsomere 1 of hind tarsus very slightly projecting ventrally (Fig. 1); male with small stout black setae on hind trochanter and posterior base of hind femur (Fig. 2). Postocellar bristles strong, at least half as long as upper orbital seta; one dorsocentral and three orbital setae present (Fig. 1) .... ***Tanypeza*** Fallén

   2 spp.: Maine to Alberta and Georgia; Steyskal 1965

   Base of tarsomere 1 of hind tarsus strongly projecting ventrally, about twice as deep as remainder of tarsomere 1 (Fig. 3); male without special setae on hind trochanter and hind femur. Postocellar bristles weak, less than half as long as upper orbital bristle; one to three dorsocentral and zero to two orbital bristles present 2

2. Only one orbital bristle present, situated at top of head; one dorsocentral bristle present ... . ***Scipopeza*** Enderlein

   Neotropical

   Two or three each of orbital and dorsocentral bristles present .... ***Neotanypeza*** Hendel

   Neotropical

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STRONGYLOPHTHALMYIIDAE

59

GEORGE C. STEYSKAL

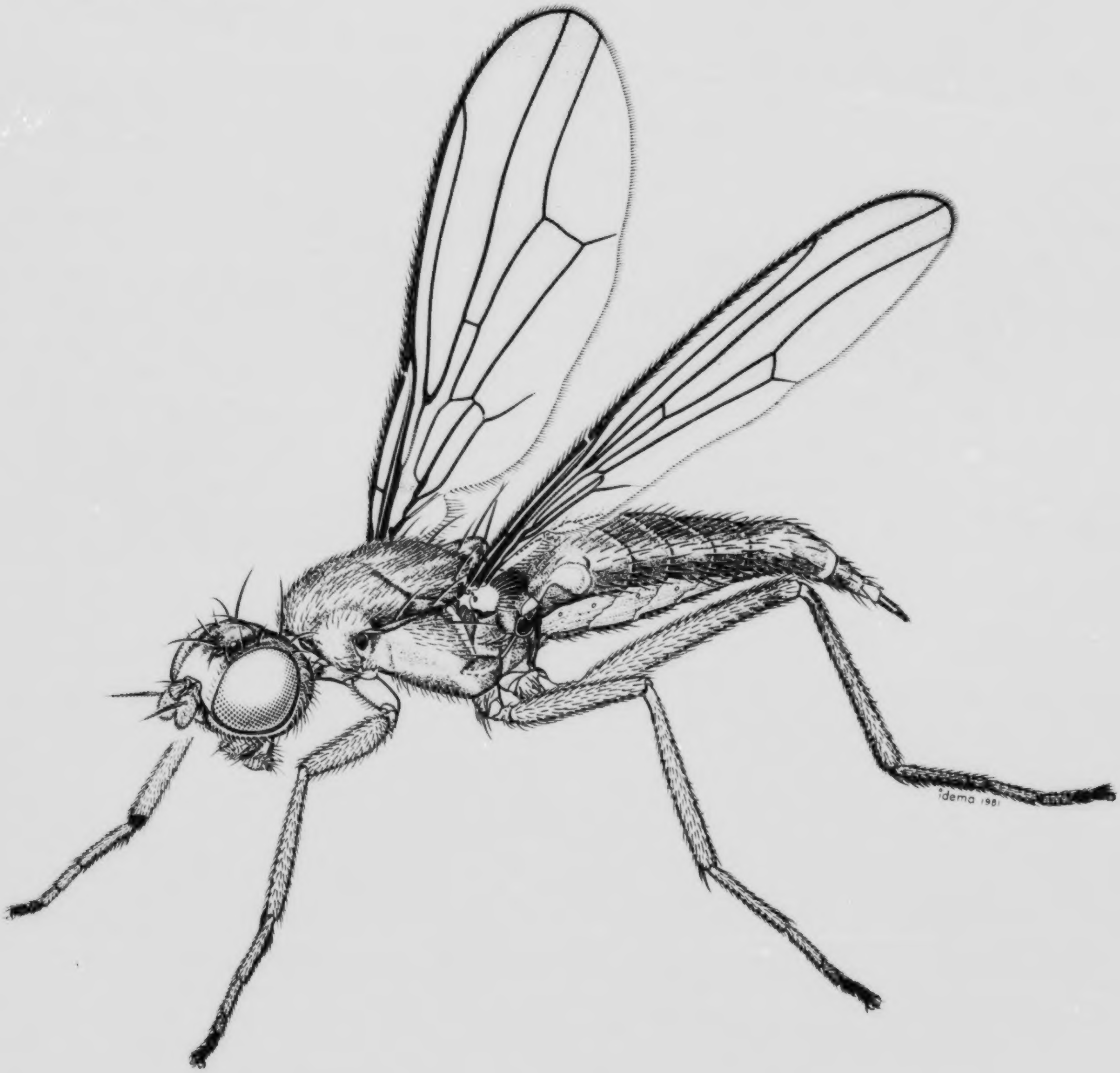
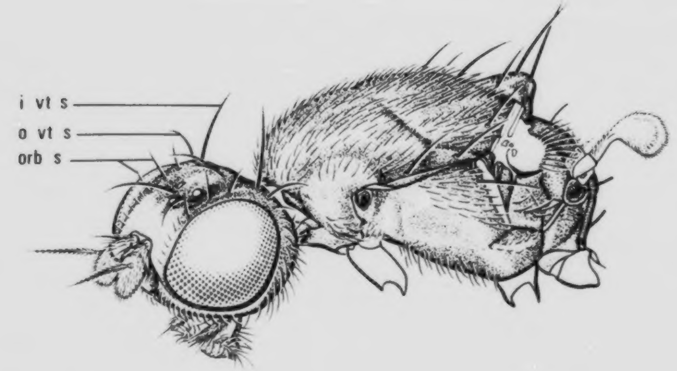


Fig. 59.1. Adult female of *Strongylophthalmyia angustipennis* Melander.

Rather slender blackish psilid-like species (Fig. 1), with yellowish legs, antenna, and anterior part of head, and with mostly hyaline weakly patterned wing. Length 3.5–4 mm. Description based on *Strongylophthalmyia angustipennis* Melander, the only species known in North America.

Adult. Head: slightly longer than high, subglobose (Fig. 2). Antenna short; first flagellomere little longer than wide, with pubescent subbasal arista. Eye large. Frons of equal width in both sexes, wider than eye at level of anterior ocellus; lower half of fronto-orbital plate with a row of setulae reaching nearly to lowermost orbital bristle (Fig. 2). Gena narrower than somewhat inflated occiput. Proboscis and palpus short. Chaetotaxy: vibrissae absent; one pair of ocellar bristles, one pair of divergent postocellar bristles, one inner and one outer vertical bristle, and three reclinate orbital bristles present.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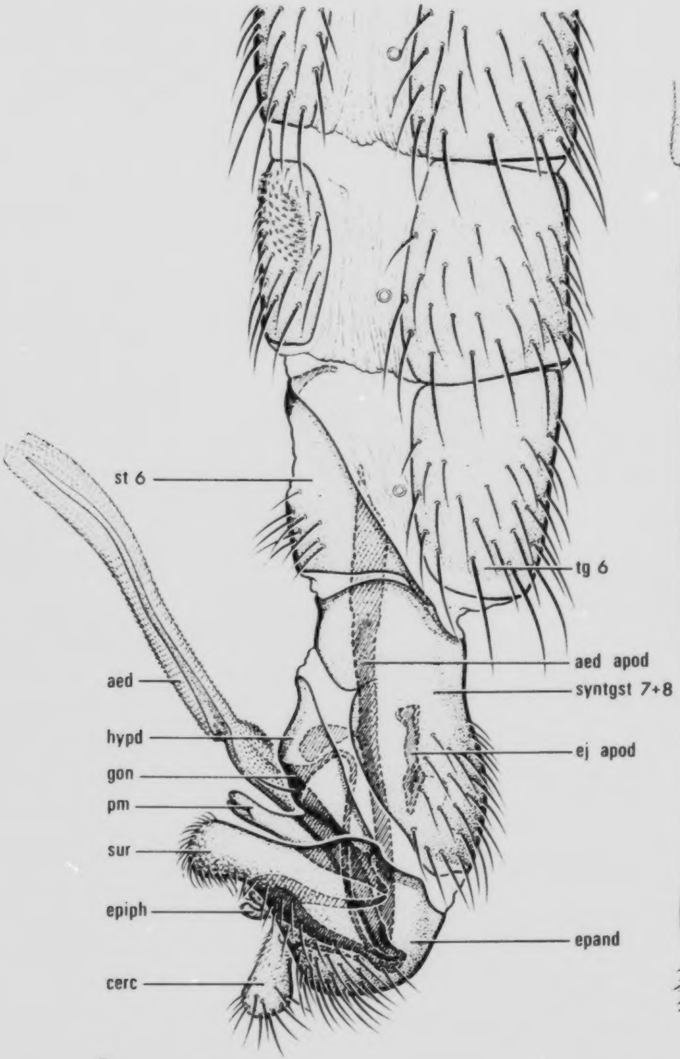
2 Strongylophthalmyia angustipennis ♀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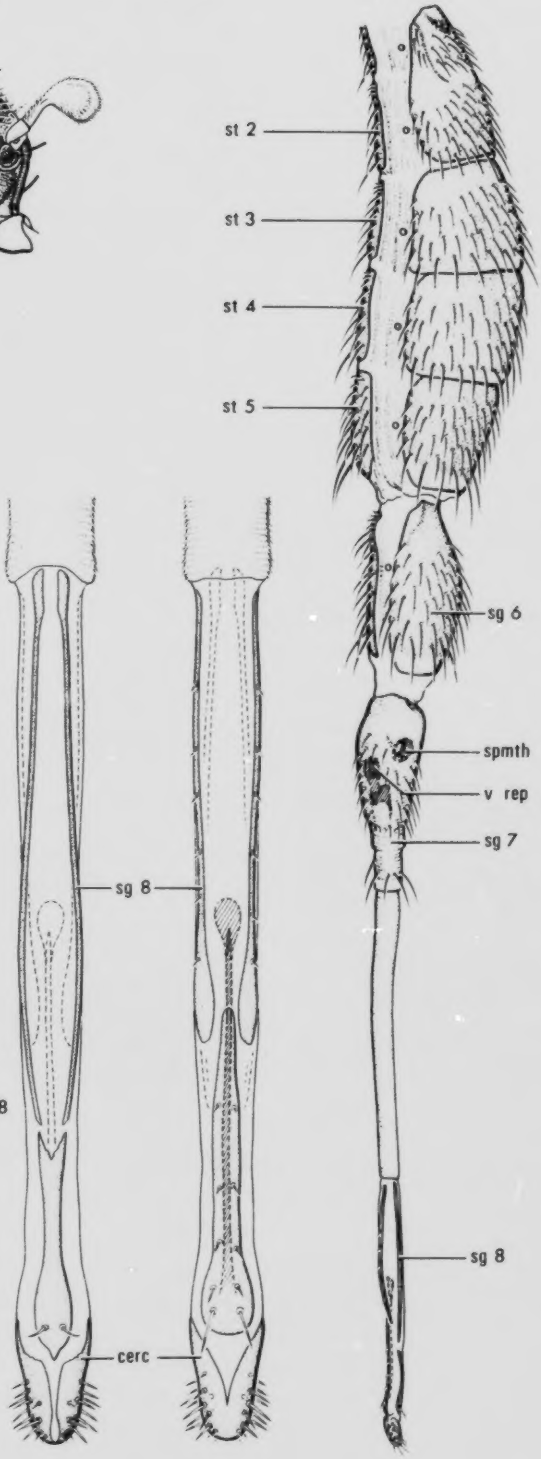
3

Strongylophthalmyia angustipennis ♂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st 5
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sg 7
sg 8
sg 8
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cerc

4 **5** **6**

Strongylophthalmyia angustipennis ♀

Thorax: nearly twice as long as wide (Fig. 2). Precoxal bridge present. Bristles difficult to distinguish from coarse yellowish hairs; two notopleural, one anepisternal, one katepisternal, several anepimeral, and only one pair of scutellar bristles distinct. Legs slender, without bristles, but with coarse hairs, and with one rather short apical bristle on mid tibia; fore coxa widely removed from mid coxa. Wing (Fig. 1) with strong subcostal break close to end of R_1; Sc discontinued a little before level of subcostal break; fork of Rs strongly divergent; cell r_3 therefore broader than cell dm; cell cu*p* about as long as cell bm, closed by circularly arcuate CuA_2; A_1 not attaining wing margin.

Abdomen: rather slender, with coarse yellowish hairs (Fig. 6).

Male terminalia (Fig. 3) with syntergosternite 7 + 8 as long as tergite 6; tergite 6 a little longer than tergite 5; sternite 6 asymmetric and joined to syntergosternite 7 + 8 in left side of abdomen. Surstylus fused to epandrium as a long lobe; rather complex epiphallus present; cerci soft; gonopod vestigial, bearing one setula. Hypandrium elongate, apically furcate, and with pair of sclerotized strips medially connected to long aedeagal apodeme; aedeagus clearly divided into basiphallus and distiphallus, and with sclerotized apical structure in some species [illustrated by Steyskal (1971) for *S. ustulata* (Zetterstedt)]; sperm pump of moderate size, with a rather slender ejaculatory apodeme.

Female abdomen (Fig. 6) rather slender; apical two-thirds of segment 7 forming a sclerotized tapered tube (ovipositor sheath); ovipositor much elongated, not adapted for piercing; cerci (Figs. 4, 5) virtually fused; one ventral receptacle and one well-developed sclerotized spermatheca present.

Classification and distribution. The family Strongylophthalmyiidae includes only the genus *Strongylophthalmyia* Heller, with 22 species in southern Asia, three in the Palaearctic region, and one each in the Malagasy subregion and the Nearctic region. Until quite recently the genus was considered to be part of the Psilidae. Griffiths (1972) placed it with the Tanypezidae, but for the reasons cited under that family, it is best treated as a distinct family. Little is known of its biology. Adults of *S. angustipennis* emerged into cages placed over felled trees at Laniel, Quebec, between June and August 1933, and several Palaearctic species have been reared from larvae found under bark of birch, elm, and aspen (Krivosheina 1981).

Steyskal (1971) gave a key to the world species and some data on the male terminalia of *S. angustipennis*, a species which is transcontinental in southern Canada and northern United States, and *S. ustulata*, which is Palaearctic. Krivosheina (1981) revised the Palaearctic species.

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Figs. 59.2–6. Details of head, thorax, and abdomen of *Strongylophthalmyia angustipennis* Melander: (2) head and thorax, left lateral view; (3) male terminalia, left lateral view; (4, 5) details of apical portion of ovipositor, dorsal and ventral views, respectively; (6) female abdomen and terminalia, left lateral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; sg, segment; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; v rep, ventral receptacle.

PSILIDAE

60

GEORGE C. STEYSKAL

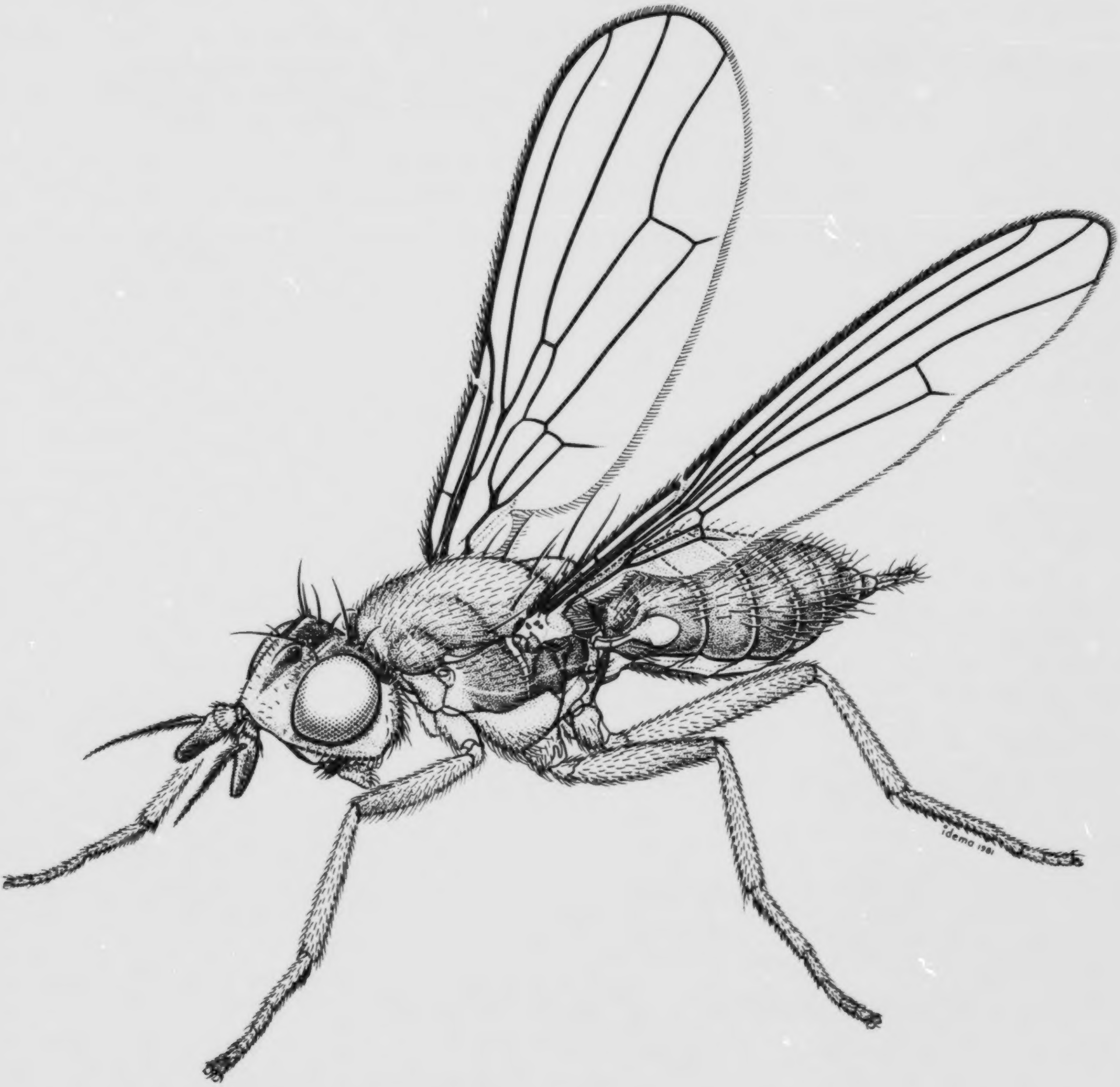


Fig. 60.1. Adult female of *Psila collaris* Loew.

Small to medium-sized flies (Fig. 1), 3–8 mm long in North American species, robust to slender, and varying in color from yellowish to reddish, brown, or black. Bristles sparse; body almost bare, except for short pile on many areas. Wing seldom distinctly patterned, but usually hyaline, yellowish, or infumated, sometimes with crossveins darkened, and with dark apical or costal seams.

Adult. Head: globular to somewhat triangular in profile, with projecting frons, and with strongly backward-sloping face (Figs. 2, 3). Eye quite large or rather small, with lower back of head appearing swollen. Antenna small or quite long; first flagellomere sometimes greatly lengthened; scape and pedicel also sometimes somewhat elongated; pedicel with a distinct dorsal seam; arista inserted subbasally or medially, short to long pubescent, and sometimes thickened. Proboscis and palpus rather small. Ocellar triangle enlarged, sometimes attaining anterior margin of frons. Chaetotaxy, when well-developed, including divergent postocellar and ocellar bristles, inner and outer vertical bristles, two orbital bristles, and no vibrissae; all except vertical bristles sometimes absent; an extra outer vertical bristle sometimes present in some species of *Psila* Meigen (Fig. 2).

Thorax: of ordinary proportions or elongate (Figs. 2, 3). Prosternum weakly sclerotized. Greater ampulla relatively distinct. Anatergal area of laterotergite sometimes prominently enlarged and callus-like (Chylizinae) (Fig. 3). Chaetotaxy: zero or one postpronotal bristle; one each supra-alar and postalar bristles; zero to six (usually one or two) dorsocentral bristles; rarely one acrostichal and one or two scutellar bristles; zero or one notopleural bristle; no pleural bristles. Legs ordinary to slender in all American species, without setae except for short apical tibial hairs; both sexes of *Loxocera* Meigen having a characteristic pad of short dense pile near tip of lower side of hind femur. Wing (Figs. 4, 5) with a broad subcostal break well before tip of R_1 and a peculiar transverse hyaline strip in the membrane severing end of Sc and extending to or beyond R_1; cell cu*p* rather elongate and squarely truncate apically; A_1 not extending to wing margin.

Abdomen: oval to elongate subparallel, without strong setae.

Male with (Figs. 6–8) tergite 6 large and free and more or less turned under laterally; sternite 6 symmetric and free, usually emarginate posteriorly; syntergosternite 7 + 8 very reduced, closely associated with epandrium; abdominal spiracle 7 present (Fig. 8) or absent (Figs. 6, 7). Epandrium not strongly turned under. Surstylus present (Chylizinae) (Figs. 6, 7) or absent (Psilinae) (Fig. 8). Hypandrium usually broad and flattened anteriorly, and connected at anterior end with aedeagal apodeme; aedeagus short and simple to long and flimsy; gonopod forming a low shoulder-like prominence on hypandrium, sometimes complex (Fig. 8). Cerci usually small and soft, sometimes fused. Sperm pump very small.

Female terminalia (Figs. 9, 10) short, soft, and little specialized, except in *Loxocera* (Fig. 10) and *Psilosoma* Zetterstedt, which have an ovipositor adapted for piercing and for which ovipositional habits are unknown. Sclerotized spermathecae lacking.

Larva. Few known; maggot-like, slender, and smooth in *Psila rosae* (Fabricius) (Hennig 1941). Anterior spiracles with several papillae in a single curved row; posterior spiracles in heavily sclerotized spiracular plates bearing a dorsal projection; three divergent slits present (Fig. 5.86).

Biology and behavior. Apparently all members of the Psilidae are phytophagous. A few species are crop pests. The carrot rust fly, *Psila rosae*, is a well-known pest of several umbellifers and other plants; other psilids affect a wide variety of plants, usually feeding as larvae in stems and roots.

Classification and distribution. The family Psilidae comprises two subfamilies: Psilinae, containing *Psila* (with several doubtfully distinct subgenera), *Psilosoma*, and *Loxocera* (with two subgenera); and Chylizinae, containing *Chyliza* Fallén (with two subgenera). Formerly, the genus *Strongylophthalmyia* Heller, now generally regarded as representing a distinct family, the Strongylophthalmyiidae (Ch. 59), was included in the Psilidae. Also, the aberrant south Chilean genus *Schizostomyia* Malloch was originally included in the Psilidae, but Hennig (1971) referred it to the Anthomyzoidea. One fossil genus and species, *Electrochyliza succini* Hennig, from Baltic amber, is known (Hennig 1965). The family is chiefly Holarctic in distribution with a few species in the Oriental, Ethiopian, and Neotropical regions. Only the Palaearctic genus *Psilosoma* does not occur in North America. Critical taxonomic work is needed on most New World species. The most recent revision of the Nearctic species is by Melander (1920); the treatment of the Palaearctic species by Hennig (1941) is also useful. A revision of the genus *Loxocera* by Capelle (1953) is more recent. The following key includes all known genera except the fossil genus *Electrochyliza* Hennig; most subgenera are also included, but several doubtful ones in *Psila* that are based mainly on weak chaetotactic characters are excluded.

Key to genera

1. Anatergal callus protruding, covered with long pile (Fig. 3). Scutellar setae in three pairs; basal pair sometimes small. Back of head nearly vertical in profile; occiput concave. Cell cu*p* distinctly shorter than cell bm (Fig. 5) ....CHYLIZINAE....***Chyliza*** Fallén....2

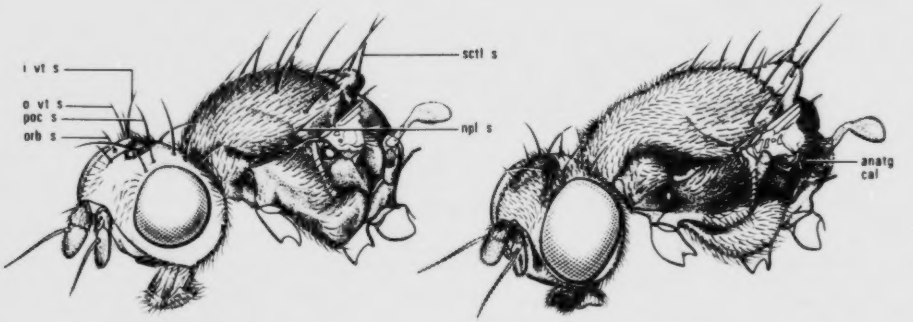
Anatergal callus gently convex to flattish, bare or with very short pile (Fig. 2). Scutellar setae in one or two pairs. Back of head in profile much inflated below; occiput seldom decidedly concave. Cell cu*p* nearly as long as cell bm (Fig. 4) ....PSILINAE....3

2. Antenna short; arista slender (Fig. 3)........................***Chyliza*** **(*Chyliza*** Fallén)
9 spp.; widespread; Melander 1920

Antenna elongate; arista thick and densely pubescent......***Chyliza*** **(*Megachetum*** Rondani)
Europe

3. Hind femur below with pad of fine dense pile near tip. First flagellomere greatly lengthened or all antennal segments elongate; antenna longer than face ....***Loxocera*** Meigen....4

Hind femur without such a pad of pile. First flagellomere seldom more than three times as long as wide and then with dense felty pubescence on arista; scape and pedicel short; antenna not longer than face 5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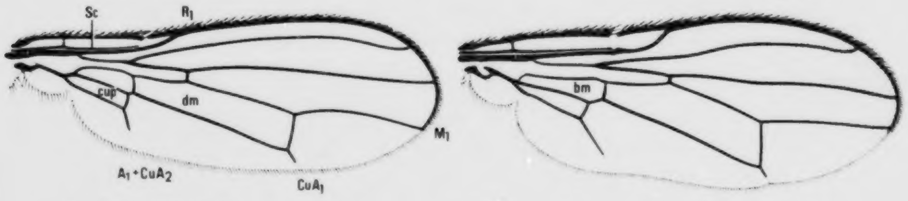
2 Psila rosae ♀ **3** Chyliza apicalis ♀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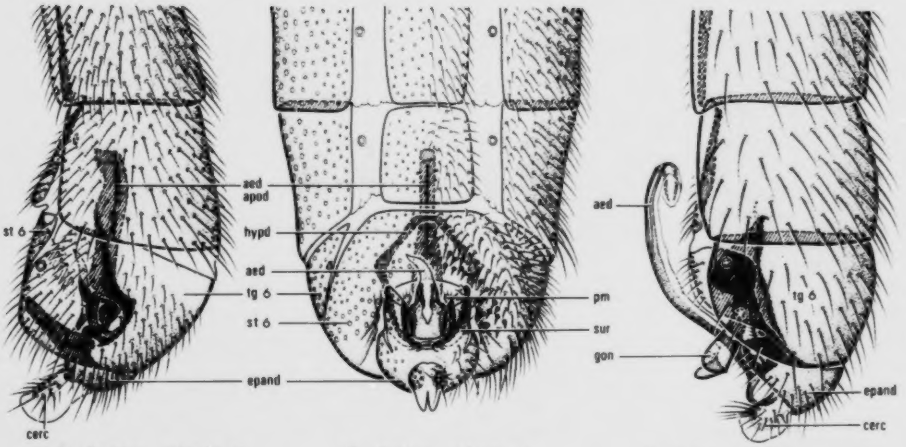
4 Psila collaris ♀ **5** Chyliza apicalis ♀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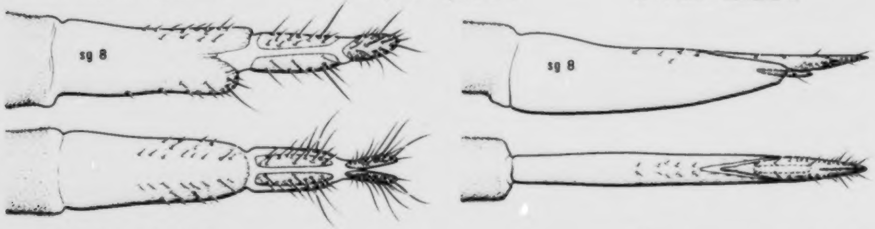
6 Chyliza apicalis ♂ **7** Chyliza apicalis ♂ **8** Psila collaris ♂



9 Psila collaris ♀ **10** Loxocera cylindrica ♀

Figs. 60.2–10. Characters: left lateral view of head and thorax of (2) *Psila rosae* (Fabricius) and (3) *Chyliza apicalis* Loew; wing of (4) *Psila collaris* Loew and (5) *Chyliza apicalis*; (6) left lateral and (7) ventral views of male terminalia of *Chyliza apicalis*; (8) left lateral view of male terminalia of *Psila collaris*; left lateral and dorsal views of ovipositor of (9) *Psila collaris* and (10) *Loxocera cylindrica* Say.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; anatg cal, anatergal callus; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; i vt s, inner vertical seta; npl s, notopleural seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; sctl s, scutellar seta; sg, segment; st, sternite; sur, surstylus; tg, tergite.

4. Scape and pedicel short; arista slender or flattened basally, tapering to slender tip and inserted near base of first flagellomere .... ***Loxocera*** **(*Loxocera*** Meigen)

5 spp.; widespread; Capelle 1953

Scape and pedicel much longer than wide; arista strongly flattened in whole length, inserted near middle of first flagellomere .... ***Loxocera*** **(*Platystyla*** Macquart)

Palaearctic

5. Notopleuron without setae. Ovipositor laterally compressed (as in Fig. 10), suited for piercing. Male with hind femur thickened and arcuate .... ***Psilosoma*** Zetterstedt

Palaearctic

Notopleuron with one seta (Fig. 2). Ovipositor neither compressed nor suited for piercing (Fig. 9). Male with simple hind femur .... ***Psila*** Meigen

16 spp.; widespread; Melander 1920, including *Pseudopsila* Johnson (with first flagellomere three times as long as wide) and other subgenera of questionable status

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DIOPSIDAE

61

B. V. PETERSON

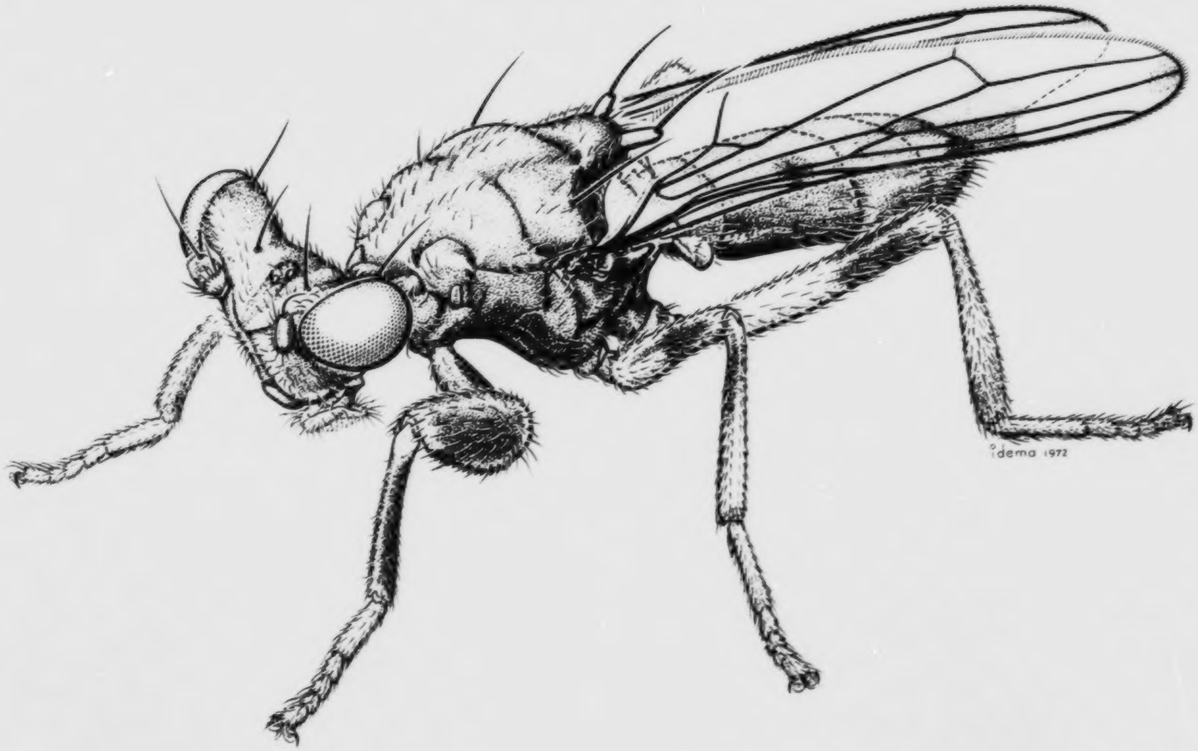


Fig. 61.1. Female of *Sphyracephala brevicornis* (Say).

Small to medium-sized flies (Fig. 1), ranging from about 4.0 to about 12.0 mm. Head subtriangular, with variably produced transverse eye stalks in all genera except the African genus *Centrioncus* Speiser. Scutellum with a pair of stout processes; laterotergite of postnotum with a dome-like swelling or spine-like process. Fore femur thickened, usually with short ventral spines or bristles.

Adult. Head: somewhat subtriangular in front view (Fig. 1), with dorsolateral margins produced laterally into short and moderately broad, or long and more slender, eye stalks that may be about as long as body; however, in *Centrioncus* head somewhat rounded, broader than long. Frons short dorsoventrally but incorporated into eye stalks laterally, bare or with few scattered fine setae, and usually with a variably developed upper orbital bristle (often wrongly called inner vertical bristle); an outer vertical bristle present posteriorly near inner margin of eye; ptilinal fissure distinct. Face long, wide, somewhat triangular in shape, moderately to strongly convex, and sometimes with a distinct medial bulge; however, face in *Centrioncus* long, relatively narrow, and flat; a distinct medial dorsoventral suture present or absent; a frontogenal suture usually evident laterally; ventrolateral margins of face rounded or produced ventrally as variably sized spine-like processes (often called facial or peristomal teeth). Clypeus short but prominent; oral vibrissae absent, but scattered fine setae sometimes present on face and gena. Antenna small; scape and pedicel short; first flagellomere roundish, with a long dorsal arista; antennae widely separated, each situated anteriorly on eye stalk near inner margin of eye; however, in *Centrioncus* antennae narrowly but distinctly separated and situated in normal position. Eye rather small, usually longer than wide and situated on apex of eye stalk, but in *Centrioncus* eye normal, not stalked, large, and higher than long; in all groups anteromedial facets near antenna slightly but distinctly enlarged; ocelli small, all subequal in size, usually on a tiny slightly raised tubercle. Proboscis short and thick; labrum about half as long as labella, strongly arched, pointed apically; hypopharynx similar in length, pointed, but more flattened; labium sclerotized medioventrally, with labella flattened; palpus short to moderately long, usually cylindrical but sometimes swollen especially dorsally, with short fine setae; lacinia stylet-like, pointed, weakly sclerotized, shorter than labrum.

Postcranium directly above occipital foramen usually with a short posteriorly directed finger-like projection bearing a raised dorsal tubercle apically that articulates in a notch-like convexity of the anterodorsal margin of the antepronotum.

Thorax: relatively short, thick, and convex (Fig. 1). Pronotum well-developed, somewhat elongate, and collar-like; antepronotum narrow, ring-like, usually with a small dorsomedial bump; postpronotum forming majority of pronotal collar, having elements of proanepisternum and proepimeron discernible in some genera; precoxal bridge complete in most genera; postpronotal lobe small but well-defined. Anterior spiracle small. Scutum projecting anteriorly between postpronotal lobes; presutural and postsutural areas of scutum strongly delineated, sometimes with a strong supra-alar spine-like process on postsutural area. Scutellum strong, convex; two apicolateral spine-like processes present, varying from moderately long to very long, and from straight to slightly or strongly curved or sinuous, bare or beset with scattered moderately long setae, and pointed apically or each bearing a short or long apical seta. Postnotum small to moderately large; each laterotergite with a dome-like swelling or a strong spine-like process or a combination of both. Chaetotaxy: scutum bare or sparsely covered by fine short or long setae, but when covered by long setae these usually also present on entire body and legs; zero or one posterior notopleural, zero or one postsutural dorsocentral, and zero or one (rarely two) postalar bristles present; fine pale setae sometimes present in postalar position when strong bristles are absent; scutellum bare or sparsely setose dorsally and sometimes ventrally, occasionally bearing two middorsolateral bristles; pleural regions of thorax bare or variously covered by sparse fine short or long setae, and lacking strong bristles. Posterior spiracle small, encircled by short fine setae.

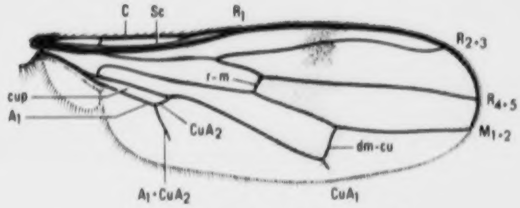
Legs moderately long, rarely very long, and usually slender. Foreleg raptorial-like; fore coxa long; fore femur variably swollen, ventrally with two rows of short spines often bordered by a series of longer bristle-like setae and sometimes with longer fine setae; fore tibia curved to fit shape and size of femur, sometimes with transverse or oblique rows of ridges and grooves on its ventral surface. First tarsomere of midleg and hindleg usually with a small cluster of bristles or a brush of fine setae basally on ventral surface. Empodia short, bristle-like; claws short, slender, and simple.

Wing (Fig. 2) slender, usually extending beyond tip of abdomen, lying flat over abdomen in resting position; anal lobe variously developed, with or without alula; membrane hyaline or patterned, densely covered with microtrichia but sometimes with a few bare patches, especially near base of wing. C without breaks, extending to M_{1+2}; Sc complete, lying close to R_1 but sometimes ending near or far from it; R_{2+3}, R_{4+5}, and M_{1+2} reaching wing margin near apex; CuA_1 and A_1 sometimes reduced or absent; cells bm and dm united; cell cu*p* moderately long, usually slender. Calypteres fringed with fine setae. Halter relatively small.

Abdomen: varying in shape from elongate cylindrical, to elongate oval, to clavate; syntergite 1 + 2 elongate, sometimes occupying more than half the total length of abdomen. Seven spiracles present in both sexes.

Female with tergite 7 sometimes complete, but usually modified so that it is emarginate anteriorly or posteriorly or both, partially divided, or completely divided into two broadly separated dorsolateral plates, and sometimes with a variably developed posteriorly directed dorsolateral arm on each side; tergites 8–10 sometimes difficult to interpret; tergite 8 usually entire but reduced, sometimes reduced to two very small dorsolateral sclerotized spots, and sometimes appearing entirely absent or fused with tergite 9; tergite 9, when distinguishable, small, sometimes appearing to be fused with tergite 8 or 10; tergite 10, when distinct, very small. Sternites sclerotized; sternite 1 reduced; sternites 2 and 3 usually largest; remaining sternites decreasing in size posteriorly; sternite 7 variable, sometimes entire, or divided into two partially or completely separated ventrolateral plates (Fig. 3), sometimes with an anterodorsal arm that unites with tergite 7, and bare or with various short spines and setae; sternite 8 with a pair of short and simple truncate to rounded apical lobes that are sometimes modified with secondary lobes, emarginations, or short spines; sternite 9 varying from completely membranous (absent), to a faintly sclerotized internal transverse or longitudinal rod-like structure, to a heavily sclerotized and more complex plate with short arm-like projections. Cercus (Fig. 3) varying from a subtriangular to a slender elongate lobe often three or four times as long as wide. Hypoproct distinct, rectangular to subtriangular, lightly sclerotized to membranous. Three, or sometimes two, small often heavily sclerotized spermathecae usually present.

Male with tergite 6 large and distinct (Fig. 4); syntergosternite 7 + 8 membranous or sclerotized, sometimes reduced to a slender sclerotized bar-like plate or to two lateral plates that articulate with small plate-like remnants of sternite 7; sternite 5 variable, complete and heavily or lightly sclerotized or membranous, sometimes reduced, or reduced to two sublateral sclerites surrounded by membrane; sternite 6 reduced, variably sclerotized or membranous, sometimes present as two small sublateral sclerites that articulate with similar sclerites of sternites 5 and 7, or sometimes reduced to two small lateral sclerotized spots; sternite 7 usually membranous, fused with syntergosternite 7 + 8 but sometimes present as two small sublateral plates that articulate anteriorly with similar plates of sternite 6 and dorsally with dorsolateral plates of syntergosternite 7 + 8. Epandrium relatively large or sometimes reduced, and sometimes uniformly rounded or modified in shape; anterior margin entire or variously emarginate; posterior margin usually cleft, with depth of cleft usually increasing with increase of size of cerci. Surstylus varying from a small simple lobe to an elongate compound lobe. Cercus varying from a small flattened lobe to a large elongate often curved lobe that may be membranous or lightly to heavily sclerotized, often with moderately long setae. Hypandrium typically a narrow or broad U-shaped sclerite, usually with short fan-like hypandrial apodemes anteriorly, and fused with gonopods; gonopods large, of various form, sometimes with setose lobes or processes of various shape and size, and sometimes asymmetric with each other, broadly fused medially or separated and joined only at inner proximal corners; parameres sometimes asymmetric with each other, varying in shape from long slender digitiform pro-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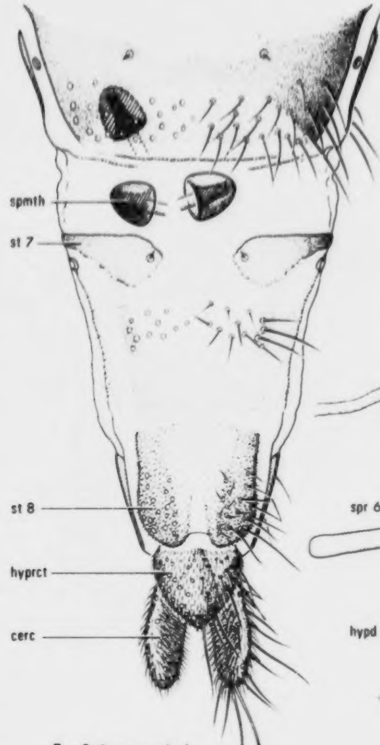
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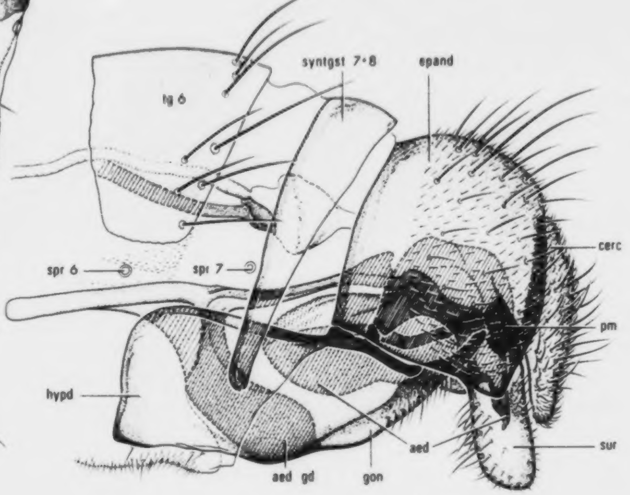
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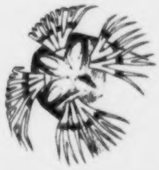
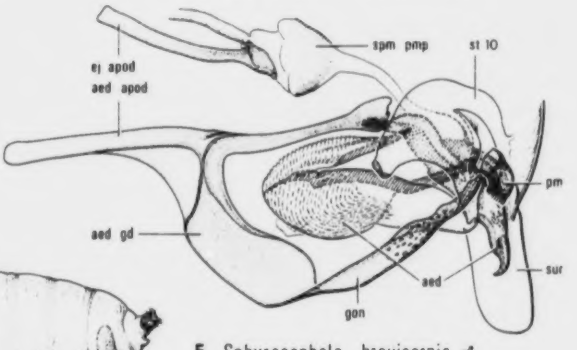


6 Sphyracephala brevicornis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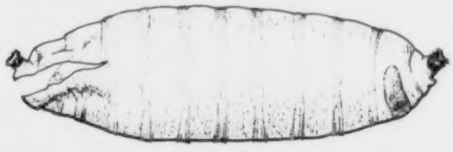
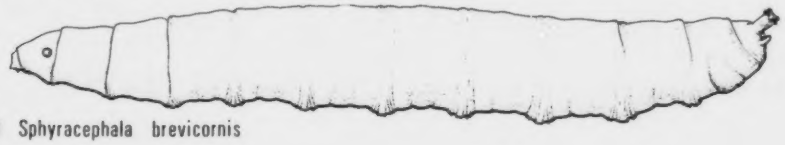


7 Sphyracephala brevicornis



8 Sphyracephala brevicornis

Figs. 61.2–8. *Sphyracephala brevicornis* (Say): (2) wing of male; terminalia of (3) female in ventral view and (4) male in lateral view; (5) internal structures of male terminalia in lateral view; (6) left posterior spiracle of larva; (7) lateral view of pupa; (8) lateral view of larva.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spm pmp, sperm pump; spmth, spermatheca; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

cesses with associated small pad-like lobes to shorter larger membranous pad-like structures with small sclerotized processes and usually with fine setae; aedeagal guide arising from point at which gonopods are joined and articulating dorsally with the aedeagal apodeme; aedeagus (Fig. 5) relatively short, with distinct basiphallus and distiphallus; distiphallus sometimes simple and sclerotized, or membranous with various sclerotized elements that may bear various setaceous structures; aedeagal apodeme usually long and heavily sclerotized; sperm pump a small subtriangular sac with a short ejaculatory apodeme attached near duct from testes.

Egg. Slender, fusiform, with one end more bluntly rounded and opposite end more narrow and somewhat pointed, about 0.60–2.20 mm long, creamy white in color. Chorion with a longitudinal, reticulate, or fishscale-like pattern. Descamps (1957) illustrated and described in detail the eggs of a number of species from North Cameroon, and Lavigne (1962) gave a brief description of the egg of *Sphyracephala brevicornis* (Say).

Larva. The following description is based on that of Lavigne (1962), who reported the only known specimen of *S. brevicornis*. This specimen was also made available for use in preparing the following description.

Slender, somewhat fusiform, tapering anteriorly, more blunt posteriorly, white except for brownish sclerotized parts and spinules (Fig. 8); cuticle smooth and shining except for creeping welts bearing spinules; length 5.5 mm; width 0.66 mm. Respiratory system amphipneustic.

Head small, retracting into thorax; mandibles and cephalopharyngeal skeleton sclerotized, darkened, extending posteriorly to metathorax. Anterior spiracles each situated on a short stalk near hind margin of prothorax, and bearing eight minute papillae arranged in a semicircle. Abdominal segments 1–8 each with a ventral creeping welt bearing a series of transverse rows of spinules; segments 1–6 each with a similar dorsal swelling also bearing transverse rows of spinules; segment 8 somewhat swollen laterally and ventrally as raised perianal pads; anal opening slit-like, with heavily sclerotized margins, and lying ventrally between perianal pads; perianal pads covered by tiny tubercles. Posterior spiracles each on a short stalk, surrounded by a plate bearing a complex series of scale-like spiracular hairs (Fig. 6).

Puparium. Subcylindrical, broader anteriorly, tapering posteriorly, darkening with age to dark brown, smooth except for spinules of larval abdominal swellings; length 3.1 mm; width 0.99 mm (Fig. 7). Anterior and posterior spiracles flattened, each situated on a short stalk.

Biology and behavior. References to the immature stages of Diopsidae are few. Risbec (1950) provided a brief note on the larva and described and illustrated the pupa of *Diopsis apicalis* Dalman. Descamps (1957) described and illustrated the larvae and puparia of several species from North Cameroon.

Little is known about the biology and life history of the Diopsidae. Houghton (1902), Flint (1956), and especially Lavigne (1962) provided what little information is known about *Sphyracephala brevicornis*, the only North American representative of the family. Sen (1921) described the life history of the Indian diopsid *Sphyracephala hearseiana* Westwood. Descamps (1957) published an extensive treatment on the fauna of North Cameroon, with an account of the biology and life history for several species. Bruggen (1961) briefly summarized Descamps' biological data and mentioned what little was known of the South African species, and Tan (1967) discussed the life histories and behavior of several Malayan species.

Some diopsid larvae are stem borers or miners in various members of the grass family (Gramineae). Several species are reported to be phytophagous, and of at least minor economic importance, in stems of rice, sugar cane, and maize. Others are reported to be saprophagous, living in decaying plant matter in moist places. Adult flies apparently feed on most any liquefied plant or animal matter and have been taken on human feces. The adults are rather poor fliers and tend to move only short distances in any one flight. Some species hibernate in protected places and others aestivate in moist places, often congregating in large numbers.

The following biological notes on *Sphyracephala brevicornis* are taken mainly from Lavigne (1962). The adults overwinter in large numbers in protected areas close to moist habitats. They emerge from hibernation on warm, sunny days as early as late March or early April and mate shortly thereafter. Neither the type of oviposition site nor the time required for ovarian development are known. However, egg development requires about 3 weeks under laboratory conditions, and the average time for larval development is about 10 days but sometimes longer. Larvae apparently feed on putrefying organic matter. Pupal development time is not known. Sen (1921) found that the pupal stage of *S. hearseiana* lasted 10–15 days and that the entire life cycle from egg to adult could be completed in about 3 weeks. Lavigne (1962) inferred that two generations of *S. brevicornis* were possible in Massachusetts. Hearsey (1844) postulated that the raptorial-like forelegs of *S. hearseiana* could be used for capturing prey. The mouthparts of the species examined for this report show no evidence of being adapted for a predatory function. It is more likely that the adults feed on plant exudates and liquefied materials of decaying plant and animal origin. Lavigne (1962) described how the enlarged forelegs of the male were used in holding the female during mating.

Additional references dealing with various aspects of the biology of the Diopsidae are cited by Shillito (1960).

Classification and distribution. The most comprehensive study on the family was made by Feijen (1984). His findings are published in a doctoral thesis (University of Leiden), which includes a number of his previously published papers. The systematic position of the family is not entirely clear. For the present, it seems best to place them, as most authors do, near the Tanypezidae, Psilidae, and Megamerinidae group of families (Diopsoidea). However, Hennig (1952) conceded that the larvae provided no support for or against the accuracy of this common assumption. Hennig further said there was no possibility of distinguishing diopsid larvae from those of other families with simple saprophagous type larvae.

A survey of the taxonomic history of the Diopsidae, along with a key to the world genera, was published by Shillito (1940). Séguy (1949) treated the species of Madagascar, and later (Séguy 1955), added three new genera to the African fauna and provided another generic key. Bruggen (1961) briefly treated the fauna of southern Africa. Shillito (1960) published a useful annotated bibliography on the Diopsidae, and in 1971, updated the historical aspects of the generic classification of the family, discussed the phylogeny in the family, and provided a revised key to the world genera. In 1972, Steyskal published a calatog of the described species and also provided a key to the world genera along with a summary of species distributions and a bibliography of useful papers published through 1971. When specimens from various parts of the world are run through both Shillito's (1971) key and Steyskal's (1972) key, they often key out to different genera; these discrepancies indicate that additional work on the generic classification is necessary.

Steyskal (1972) listed 153 world species in 13 genera. These are distributed mainly in Africa, the Oriental region, and Malagasy; only a few species are known from Arabia and the Palaearctic and Nearctic regions.

Sphyracephala brevicornis is the only known Nearctic species of Diopsidae. It is interesting to note that it was the first fly to be described by a North American entomologist (Stone 1980).

Two fossil species of *Prosphyracephala* Hennig have been recorded from Baltic amber (Meunier 1903, Bachofen-Echt 1949, Hennig 1965); however, Hennig (1969) suggests the possibility that *P. breviata* (Meunier) may be a synonym of *P. succini* (Loew). One species, *P. rubiensis* Lewis, has been recorded from late Oligocene shale deposits of southwestern Montana (Lewis 1971).

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LONCHAEIDAE

62

J. F. MCALPINE

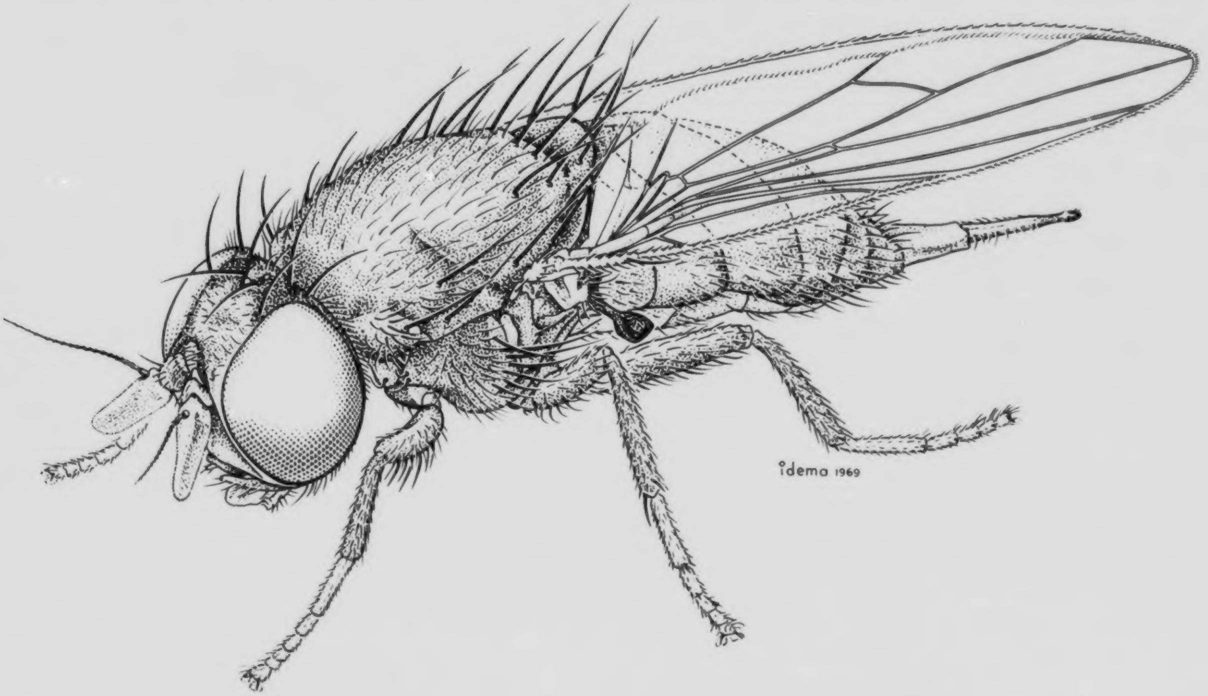
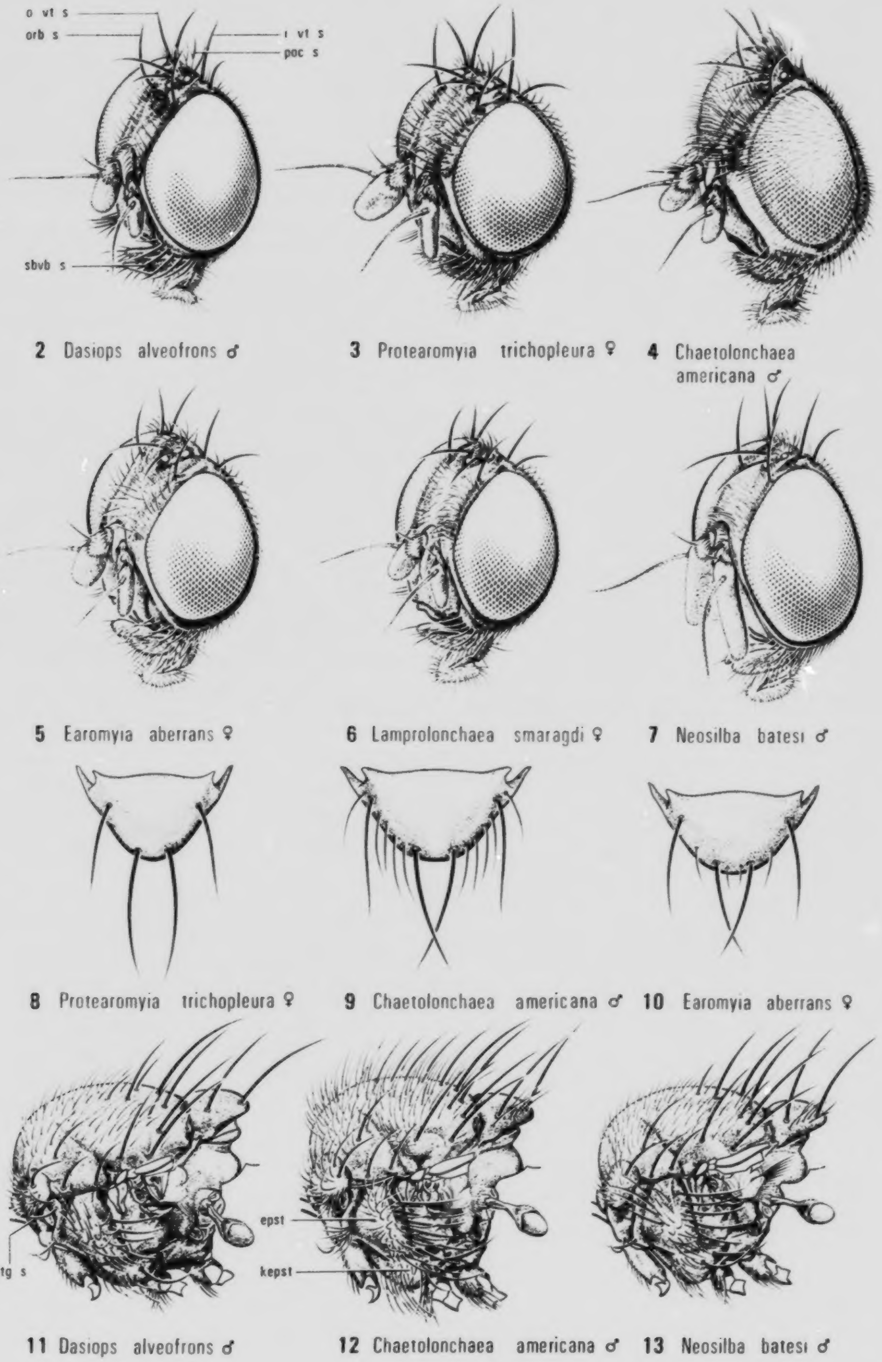


Fig. 62.1. Adult female of *Lonchaea polita* Say.

Stout-bodied hairy flies (Fig. 1), 3-6 mm long, usually shining blue black, sometimes dull brown, with a wide high head and a broad flat abdomen. Wing usually clear, occasionally yellowish to brownish fumose. Halter black.

Adult. Head: frons (Figs. 2–7) narrower in male than in female; interfrontal area strongly sclerotized and hairy; orbital plate reaching one-quarter to one-third distance from vertex to lunule; lunule large, exposed, and bare or setulose. Face broad, depressed, usually without strong facial carina or antennal grooves. Chaetotaxy: a single reclinate orbital bristle present; ocellar and inner and outer vertical bristles strong; postocellar bristles divergent, rather weak; one to several rows of subvibrissal hairs present below eyes; no distinct vibrissae present, but sometimes one or more subvibrissal hairs enlarged and vibrissa-like. First flagellomere short and porrect to long and decumbent, black to yellowish orange; arista bare to pubescent or plumose. Palpus moderately large, fairly broad, flattened at apex. Compound eye large, round to high oval, pilose or bare.

Thorax: scutum (Figs. 11–13) rather strongly arched, always black or brown in background color, pruinose to highly polished; setulae, hairs, and bristles fairly dense and strong. Chaetotaxy: one postpronotal, one presutural supra-alar, two notopleural, one postsutural supra-alar, two postalar, two postsutural dorsocentral, and two prescutellar acrostichal bristles present; a weak postsutural intra-alar bristle also frequently present; scutellum (Figs. 8–10) with four marginal bristles, i.e. an anterior pair and a posterior pair, with or without additional hairs on margins, apex, and disc; proepisternum with a single bristle; proepimeron with one to many hairs; declivity above anterior spiracle with (Fig. 11) or without (Figs. 12, 13) poststigmatal bristles; katepisternum with one to three bristles and numerous setulae; anepisternum with numerous hairs and bristles, sometimes without anterodorsal ones but always with posterior ones; anepimeron usually bare, sometimes with one to several hairs in middle; meron bare. Prosternum usually bare, sometimes with a few fine hairs at side; metasternal area bare.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7 Neosilba batesi ♂
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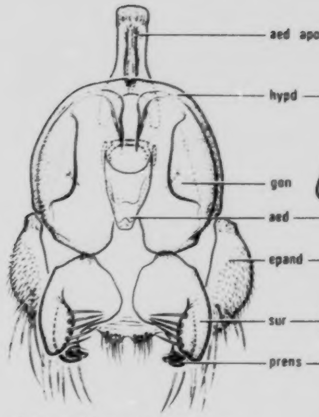
12 Chaetolonchaea americana ♂
13 Neosilba batesi ♂

Figs. 62.2–13. Heads and thoraces: heads of (2) *Dasiops alveofrons* McAlpine, (3) *Protearomyia trichopleura* McAlpine, (4) *Chaetolonchaea americana* McAlpine, (5) *Earomyia aberrans* (Malloch), (6) *Lamprolonchaea smaragdi* (Walker), and (7) *Neosilba batesi* (Curran); dorsal views of scutellum of (8) *Protearomyia trichopleura*, (9) *Chaetolonchaea americana*, and (10) *Earomyia aberrans*; left lateral views of thorax of (11) *Dasiops alveofrons*, (12) *Chaetolonchaea americana*, and (13) *Neosilba batesi*.

Abbreviations: epst, episternum; i vt s, inner vertical seta; kepst, katepisternum; orb s, orbital seta; o vt s, outer vertical seta; poc s, postocellar seta; pstg s, poststigmatal seta; sbvb s, subvibrissal seta.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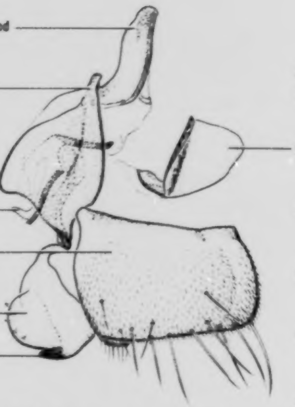
14 Dasiops alveofrons ♂



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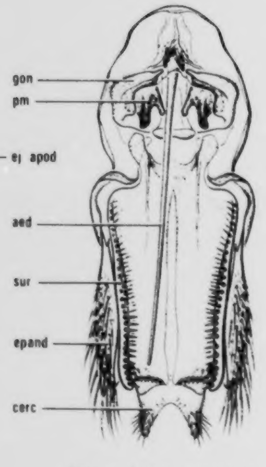
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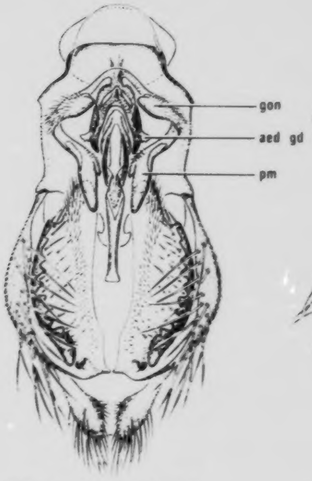
16 Neosilba batesi ♂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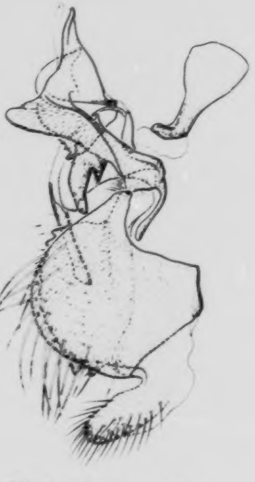
17 Lonchaea polita ♂



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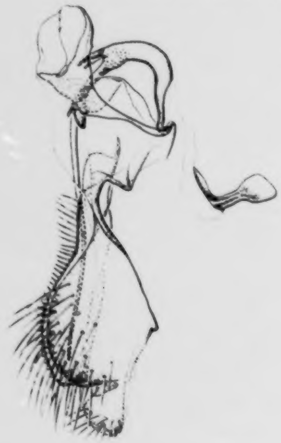
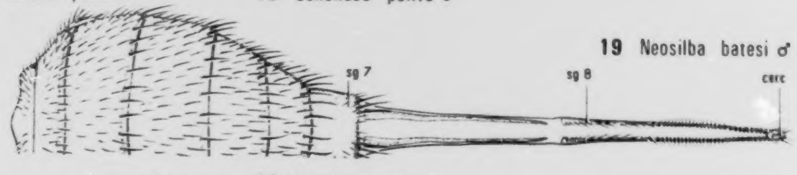


19 Neosilba batesi ♂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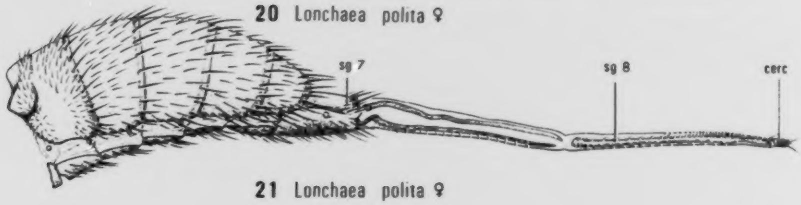
20 Lonchaea polita ♀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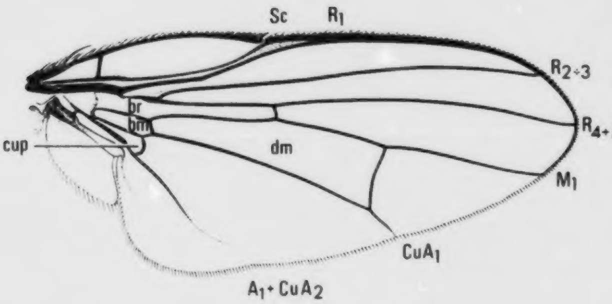
21 Lonchaea polita ♀

Figs. 62.14–21. Terminalia: (14) ventral and (15) left lateral views of male terminalia of *Dasiops alveofrons* McAlpine; (16) ventral and (19) left lateral views of male terminalia of *Neosilba batesi* (Curran); (17) ventral and (18) left lateral views of male terminalia of *Lonchaea polita* Say; (20) dorsal and (21) left lateral views of female abdomen and terminalia of *Lonchaea polita*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; prens, prensiseta; sg, segment; sur, surstylus.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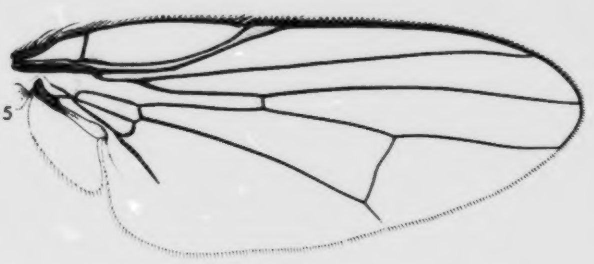
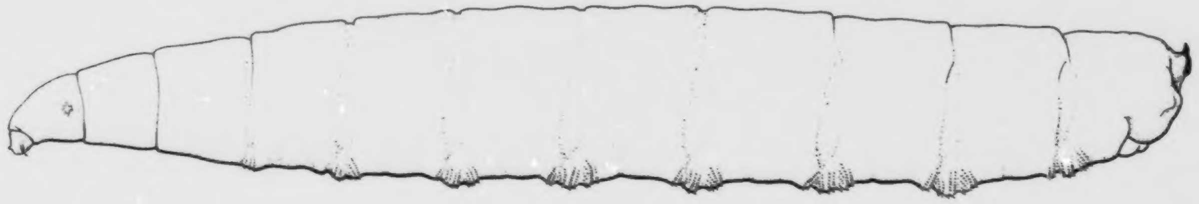
A1+CuA2

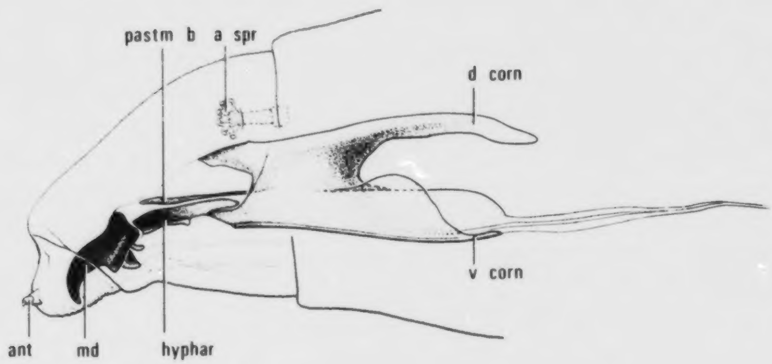
22 Lonchaea polita ♂



23 Dasiops alveofrons ♂



24 Lonchaea corticis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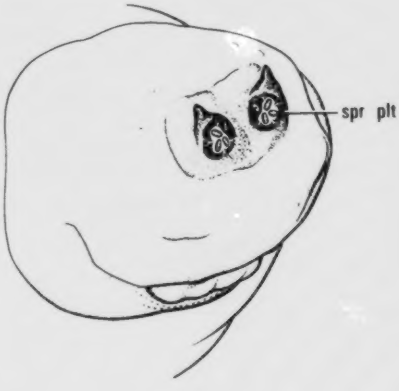
25 Lonchaea corticis



26 Lonchaea corticis

Figs. 62.22–26. Wing and larva: wing of (22) *Lonchaea polita* Say and (23) *Dasiops alveofrons* McAlpine; (24) mature larva of *Lonchaea corticis* Taylor, left lateral view; (25) mouthparts of L. *corticis*, left lateral view; (26) posterior end of *L. corticis*, left posterolateral view.

Abbreviations: ant, antenna; a spr, anterior spiracle; d corn, dorsal cornu of tentoropharyngeal sclerite; hyphar scl, hypopharyngeal sclerite; md, mandible; pastm b, parastomal bar; spr plt, spiracular plate; v corn, ventral cornu of tentoropharyngeal sclerite.

Wing (Figs. 22, 23) rather strongly tapered from base to apex, i.e. anal lobe and alula well-developed. C extending to M, constricted but not completely broken at position of humeral and subcostal breaks; Sc complete and free from R_1; pterostigmal section (between insertions of Sc and R_1) short to long; cells bm and dm separated; cell cu*p* present; A_1 continuing to or near to wing margin as a fold (Fig. 22) or not (Fig. 23). Upper calypter well-developed, with whitish to brownish margins and fringes; cilia at calyptral fold often longer, stronger, and darker than others. Halter entirely blackish.

Legs stocky; coxae, femora, and tibiae blackish; tarsi yellow to black. Femora rather swollen with many hairs and bristles. Tibiae with many rows of setulae but very few bristles; preapical dorsal bristle usually indistinguishable except occasionally on mid tibia; apicoventral bristle present on mid tibia.

Abdomen: broad and flat (Fig. 20). Seven pairs of spiracles in membrane adjacent to respective tergites and sternites.

Male terminalia (Figs. 14–19) with tergite 6 present in some *Dasiops* Rondani, otherwise absent or indistinguishably fused with tergite 5; sternite 6 varying from well-developed, symmetric, separate, and in a ventral position to reduced, asymmetric, fused with sternites 7 and 8, and shifted to a laterodorsal position on left side. Tergite 9, the epandrium, and sternite 9, the hypandrium, and associated structures symmetric; gonopod with base broadly fused to hypandrium, always with a tiny setula on inner face near apex; paramere reduced and semimembranous (Fig. 14) to strongly developed and toothed (Figs. 16, 17); aedeagal guide sometimes fairly elaborate (Fig. 17); surstylus articulated with lateral margins of epandrium, pendulant in *Dasiops* (Figs. 14, 15) and some *Protearomyia* McAlpine, at least partially enclosed within lateral margins of epandrium in other genera (Figs. 16–19), with (Fig. 14) or without (Fig. 17) strong prensisetae. Aedeagus short, unsegmented, and spout-like in *Dasiops* (Fig. 14) to elongate, bisegmented, and ornamented in other genera (Figs. 16–19). Cerci in form of simple lobes that are usually flap-like, variously sclerotized, and hairy, but tooth-like and bare in *Chaetolonchaea* Czerny.

Female (Figs. 20, 21) with abdominal sternite 6 and sometimes sternite 5 with a median anteriorly directed apodeme arising from anterior margin; tergite 7 and sternite 7 fused laterally, each with a pair of long flexible strap-like extensions from posterior margin. Segment 8 in form of four elongate rods that make up main shaft of ovipositor; cerci fused to form short, variously shaped, and bristled apical segment of ovipositor; three spermathecae present, usually elongate and wrinkled, but sometimes bell-shaped or spherical and smooth.

Larva. Slender, rather peg-shaped in outline (Fig. 24), smooth except for ventral creeping welts. Cephalopharyngeal skeleton (Fig. 25) consisting of following paired structures: a stout untoothed mandible (mouth hook), a quadrangular to triangular dental sclerite, an elongate hypopharyngeal sclerite, a slender parastomal bar, and a more or less anvil-shaped tentoropharyngeal sclerite. Anterior spiracles each with five to ten papillae arranged fan-wise (Fig. 25). Posterior spiracles (Figs. 24, 26) each on a raised heavily sclerotized stump-like posterior spiracular tubercle; each spiracular plate usually with a dorsolateral lobe or ridge; each spiracle with three oval radially arranged slits and four groups of branched spiracular hairs.

Biology and behavior. Larvae of Lonchaeidae are mainly followers of decay in vegetation, but a few species are primary invaders of plant tissue. A great variety live in injured fruits, vegetables, cacti, and other decaying organic matter. Many species of *Dasiops* and *Lonchaea* Fallén live under bark of dead or dying trees, especially conifers, often in association with bark beetles and weevils; some species of *Earomyia* Zetterstedt live in cones, probably mostly in association with Cecidomyiidae and other primary invaders; others live in flower heads and root crowns.

Classification and distribution. The family has two subfamilies, Dasiopinae and Lonchaeinae, and contains nine genera; all genera occur in or adjacent to the Nearctic region. The genus *Lamprolonchaea* Bezzi has a mainly Ethiopian and Oriental distribution, but one species, *smaragdi* (Walker), (=*aurea* (Macquart)), has been intercepted in Bermuda; it is not known if it is or is not established there. Likewise, the genus *Silba* Macquart is primarily Ethiopian and Oriental in distribution, but at least one species, *S. devians* Hennig, occurs in South America (McAlpine and Steyskal 1982). In all, there are probably about 200 Nearctic species in the family, many of them still undescribed. No fossil Lonchaeidae is known. *Lonchaea senescens* Scudder, from Tertiary shales in British Columbia, was assigned to Lauxaniidae (McAlpine 1962). *Glaesolonchaea electrica* Hennig and *Morgea mcalpinei* Hennig, both described from Baltic amber and originally assigned to the Lonchaeidae (Hennig 1967), were subsequently found to belong to the Pallopteridae (Morge 1967, McAlpine 1981).

Key to genera

1. Poststigmatal bristles present (Fig. 11) .... DASIOPINAE....***Dasiops*** Rondani
about 50 species; McAlpine 1964*a* (descriptions)
Poststigmatal bristles absent (Figs. 12, 13) .... LONCHAEINAE....2

2. Lunule bare (Figs. 3–6) .... EAROMYIINI....3
Lunule setulose (Figs. 2, 7) .... LONCHAEINI....6

3. Scutellum with four bristles only, without additional hairs or setulae (Fig. 8) .... ***Protearomyia*** McAlpine

3 spp.; McAlpine 1983 (world revision)

Scutellum with two or more hairs or setulae in addition to usual four bristles (Figs. 9, 10) 4

4. Body brilliant golden green or bronzy blue. Eye bare. Hairs of frons sparse and short (Fig. 6). Anepisternum with one to several clearly distinguishable anterodorsal bristles and two such posterodorsal bristles (as in Fig. 13). Katepisternum with one clearly distinguishable bristle .... ***Lamprolonchaea*** Bezzi

1 sp., *smaragdi* (Walker) (=*aurea* (Macquart)); intercepted in Bermuda

Body dull to subshining brownish black or bluish black. Eye frequently pilose. Hairs of frons fairly dense and long (Figs. 4, 5). Anterodorsal bristles of anepisternum present (as in Fig. 13) or absent (Fig. 12); posterior bristles more numerous, sometimes indistinguishable from hairs. Katepisternum usually with several bristles 5

5. Scutellum with one or more marginal hairs anterior to basal scutellar bristles (Fig. 9); anterodorsal bristles of anepisternum weak or absent (Fig. 12). Cheek and parafacial wide (Fig. 4). Calypteres with whitish margins and fringes .... ***Chaetolonchaea*** Czerny

1 sp., *americana* McAlpine; western Canada and U.S.A.; McAlpine 1982 (world revision)

Scutellum bare anterior to lateral scutellar bristle (Fig. 10); anterodorsal bristles of anepisternum long (as in Fig. 13). Cheek and parafacial usually narrower (Fig. 5). Calypteres always with brown margins and fringes .... ***Earomyia*** Zetterstedt

8 spp.; McAlpine 1956 (key to Nearctic cone-infesting species)

6. Katepisternum with one strong bristle (Fig. 1). Arista usually bare or shortly pubescent .... ***Lonchaea*** Fallén, in part

about 70 spp.; McAlpine 1964*b* (descriptions), McAlpine 1970 (key to Nearctic members of *corticis* group)

Katepisternum with two strong bristles (Fig. 13). Arista bare to long plumose 7

7. Arista usually bare or shortly pubescent; if arista somewhat long pubescent, then fringes of calypteres uniform in length. Prosternum bare 8

Arista plumose (Fig. 7); if arista somewhat shortly plumose, then fringes of calypteres with a cluster of long blackish setae at fold (Fig. 13). Prosternum bare or setulose 9

8. Abdominal sternite 1 setulose .... ***Setisquamalonchaea*** Morge

1 sp., *fumosa* (Egger); introduced from Eurasia

Abdominal sternite 1 bare .... ***Lonchaea*** Fallén, in part

see couplet 6

9. Fringes of calypteres with a cluster of long blackish setae at fold (Fig. 13). Posterior margin of anepisternum with five to seven evenly spaced bristles (Fig. 13). Prosternum usually bare .... ***Neosilba*** McAlpine

mainly Neotropical, several species in southernmost Nearctic region; McAlpine and Steyskal 1982

Fringes of calypteres uniform throughout (as in Figs. 11, 12). Posterior margin of anepisternum with three or four strong bristles, with a gap in middle. Prosternum always setulose .... ***Silba*** Macquart

mainly Old World tropics, not yet known in Nearctic region

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OTITIDAE

63

GEORGE C. STEYSKAL

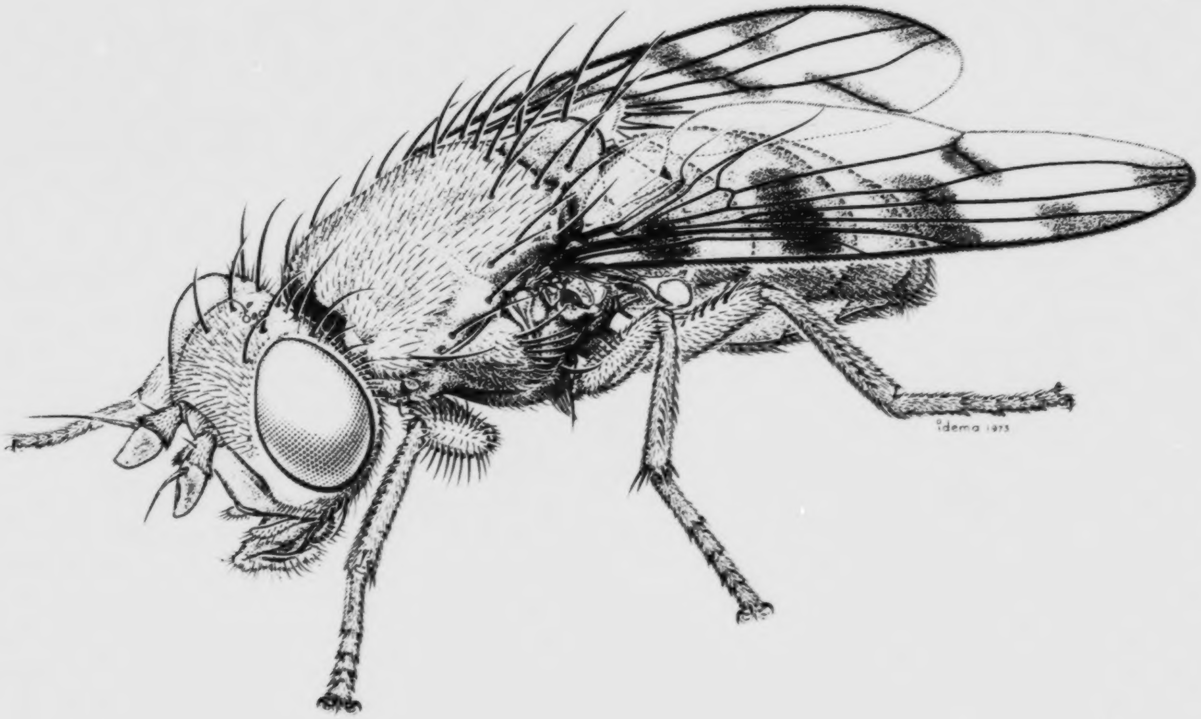


Fig. 63.1. Adult male of *Ceroxys latiusculus* (Loew).

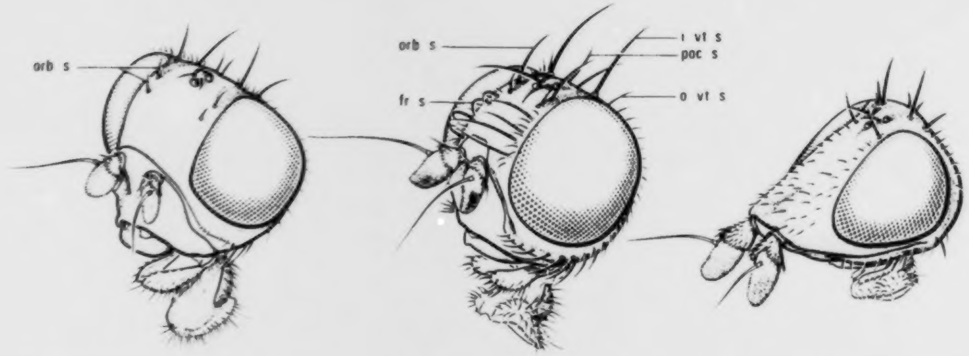
Flies (Fig. 1) of quite varied habitus, but never exceptionally elongate nor compact, although a few species slender enough to mimic ants; length 3–12 mm in North American species. Coloration often quite bright and frequently metallic. Wing usually with some kind of pattern.

Adult. Head: variously shaped (Figs. 2–10), usually higher than long, but in *Eumetopiella* Hendel (Fig. 4) nearly twice as long as high. Bristles reduced in number, but inner and outer vertical bristles and ocellar, divergent postocellar, and one or two orbital bristles usually present; frontal bristles sometimes well-developed (Fig. 3). Frons sometimes pitted or wrinkled (Fig. 6); lunule usually narrowly exposed and bare. Face fully sclerotized in middle, usually broad and convex, sometimes with a prominent median carina and deep antennal grooves (Fig. 9). Parafacials nearly linear to very broad. Clypeus moderately large; gena narrow to very broad; vibrissa absent. Antenna (Figs. 11–14) of various sizes and shapes; first flagellomere sometimes elongate and often with sharp tip (Fig. 13); arista slender, bare to plumose. Proboscis and palpus ordinary, usually rather stout.

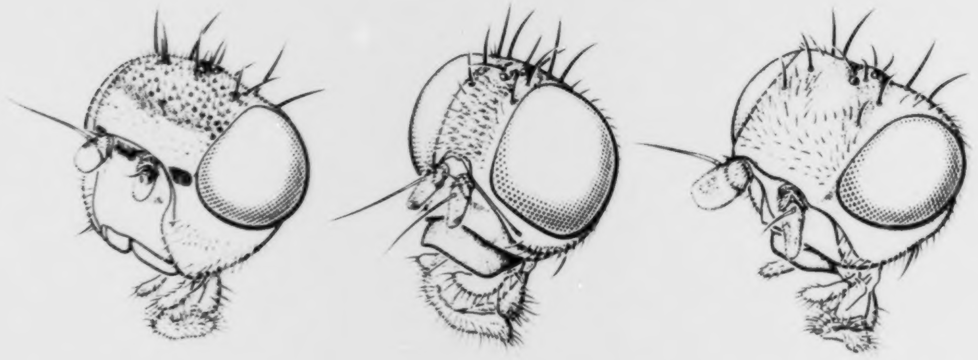
Thorax: usually somewhat longer than broad. Chaetotaxy variable; notopleuron with two bristles; katepisternal bristle present, except in *Myrmecothea* Hendel; proepisternal bristle absent to well-developed; presutural dorsocentral bristles sometimes present (*Dyscrasis* Aldrich and *Melieria* Robineau-Desvoidy). Wing (Figs. 15–22) variously shaped; Sc complete, curving forward to end in C; R_1 setose or bare; cell cu*p* (lacking in *Steneretma* Loew, Fig. 17), with anterior side usually less than 0.25 as long as posterior side of cell dm, but if longer usually with pointed or extended posterior apex. Legs moderately developed; fore femur sometimes with strong ventral bristles.

Abdomen: variously shaped (Figs. 23–29), sometimes petiolate in ant-mimicking species. Seven spiracles present in female and five in male.

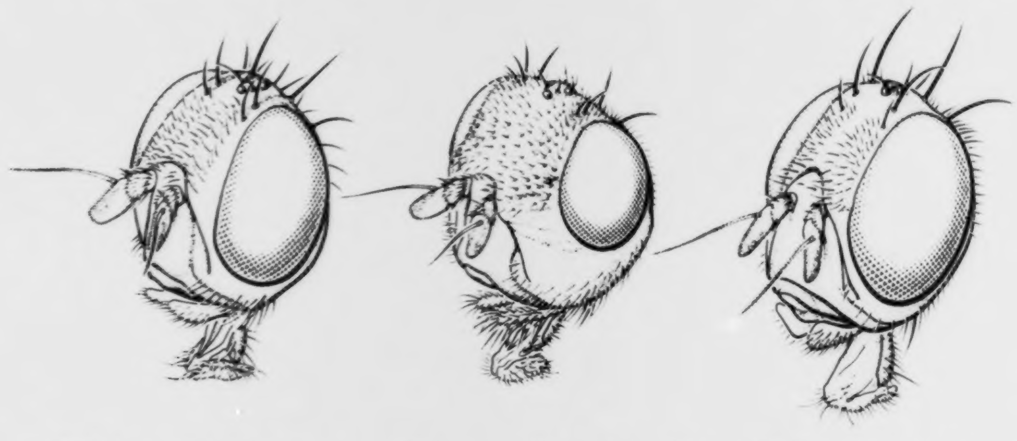
Terminalia of male (Figs. 23–26) with epandrium neither extended ventrally nor enfolding surstyli. Hypandrium with gonopod and paramere reduced, frequently atrophied or indistinguishable; epiphallus sometimes conspicuously developed and resembling surstylus; aedeagal apodeme cuneiform or Y-shaped, not fused with hypandrium; aedeagus



2 Physiphora demandata ♀ 3 Chaetopsis fulvifrons ♀ 4 Eumetopiella rufipes ♀



5 Oedopa capito ♀ 6 Acrosticta apicalis ♀ 7 Homalocephala similis ♀



8 Herina canadensis ♀ 9 Tetanops (Eurycephalomyia) myopaeformis ♀ 10 Delphinia picta ♀

Figs. 63.2–10. Heads: (2) *Physiphora demandata* (Fabricius); (3) *Chaetopsis fulvifrons* (Macquart); (4) *Eumetopiella rufipes* (Macquart); (5) *Oedopa capito* Loew; (6) *Acrosticta apicalis* (Williston); (7) *Homalocephala similis* (Cresson); (8) *Herina canadensis* (Johnson); (9) *Tetanops* (*Eurycephalomyia*) *myopaeformis* (Röder); (10) *Delphinia picta* (Fabricius).

Abbreviations: fr s, frontal seta; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; poc s, postocellar seta.

with complex or simple end-structure, but without pair of apical projections; aedeagal stem bare (Figs. 23, 24) or with teeth, bristles, or hairs (Figs. 25, 26); sperm pump with membranous vesicle.

Terminalia of female (Figs. 27—29) with segment 7 dorsoventrally flattened, forming a more or less triangular or keystone-shaped oviscape. Ovipositor sword-like, sometimes broadened, depressed, and forming a sharp piercer. Three sclerotized spermathecae usually present (Fig. 29); two in *Euxesta notata* (Wiedemann) (Figs. 27, 28).

Larva. Resembling those usually found in acalyptrate Diptera (Figs. 30-33), with fan-shaped anterior spiracle and three more or less radially disposed slit-shaped openings in each posterior spiracular plate (Fig. 31). No features known to distinguish them from Tephritidae, Platystomatidae, and some species of Lonchaeidae.

Immature stages of only a few North American species have been described. A review of literature was given by Allen and Foote (1967) and Valley *et al*. (1969), who also described in detail larvae of a few species.

Biology and behavior. The references cited above also review the biology of North American Otitidae. The family is apparently mostly saprophagous, but the phytophagous habit has been developed in a few species, including some of economic importance. Several species are known to develop under the bark of dead trees (Teskey 1976); some have been found in manure and decaying vegetation, probably invading living tissue of the latter; confirmed phytophagous species are *Tetanops* (*Eurycephalomyia*) *myopaeformis* (Röder) in sugar beets and *Tritoxa flexa* (Wiedemann) in onions. A few species of *Euxesta* Loew have been reared from ears of maize, but damage to kernels has not been definitely confirmed. Valley *et al*. (1969) describe the larva of *Eumetopiella rufipes* (Macquart) as feeding on peduncles and on developing inflorescences of barnyard grass, *Echinochloa crusgalli* (L.) Beauv.

Classification and distribution. The Otitidae are predominantly of north temperate distribution. The subfamily Ulidiinae, however, is well represented in the tropics; the center of distribution of the genus *Physiphora* Fallén is evidently in Africa and that of *Euxesta*, in South America. The two subfamilies Otitinae and Ulidiinae have been considered as distinct families, but Hennig (1939, 1940), in his revisions of the Palaearctic species, and in his later more general treatment (Hennig 1973), has shown that the only thoroughgoing distinction between them lies in the aedeagus. Therefore, they are considered as subfamilies here as in my earlier paper (Steyskal 1961). These two subfamilies can be separated by characteristics of the aedeagus and wing vein R_1. In the Otitinae the aedeagus is bristly or hairy or has teeth or blades on the stem, and the tip is more or less simple (Figs. 25, 26). The aedeagus is bare in the Ulidiinae and the end structure is sometimes specialized (Figs. 23, 24). In the Otitinae the upper side of wing vein R_1 is setulose apically (Figs. 19-22), except in *Curranops* Harriot (some species), *Notogramma* Loew, *Seioptera* Kirby, *Tujunga* Steyskal, and *Ulidiotites* Steyskal. In Ulidiinae this vein is bare (Figs. 15-17), except in *Homalocephala* Zetterstedt and in some species of *Euxesta* and *Acrosticta* Loew. No fossils are known.

Key to genera

1. Katepisternal bristle absent. (Wing narrow, with R_1 setulose apically; alula absent (Fig. 19). Proepisternal bristle very small; one pair of scutellar bristles present. Form ant-like) . . . . ***Myrmecothea*** Hendel
1 sp., *myrmecoides* (Loew); eastern North America

Katepisternal bristle present, although weakly so in *Homalocephala* 2

2. Cell cu*p* lacking; wing less than 0.25 as wide as long (Fig. 17) . . . . ***Steneretma*** Loew
1 sp., *laticauda* Loew; central and southeastern U.S.A.

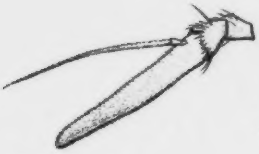
Cell cu*p* present (Figs. 15, 16, 18-22); wing usually broader than described above 3

3. Wing less than 0.33 as wide as long, with little color pattern; cell cu*p* without extension (Fig. 20). (Proepisternal bristle small or lacking. Body without metallic coloration. Form ant-like) 4

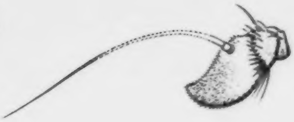
Wing at least 0.33 as wide as long or body metallic-colored (*Eumetopiella*), often with extensive color pattern 5

4. Frons with narrow but distinct dull median stripe. Wing 0.31 as wide as long; crossvein r-m at midlength of wing; color hyaline, with apical dark spot . . . . ***Cephalia*** Meigen
4 spp.; western mountains

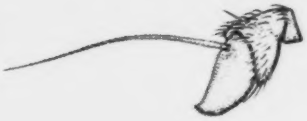
Frons wholly shining. Wing 0.25 as wide as long; crossvein r-m at 0.66 of distance from base to apex of wing; color brownish with subapical transverse hyaline bar (Fig. 20) . . . . ***Myiomyrmica*** Steyskal
1 sp., *fenestrata* (Coquillett); central U.S.A.



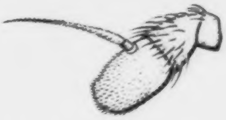
11 Stictomyia longicornis ♀



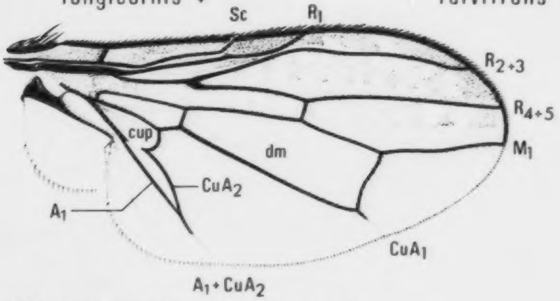
12 Chaetopsis fulvifrons ♀



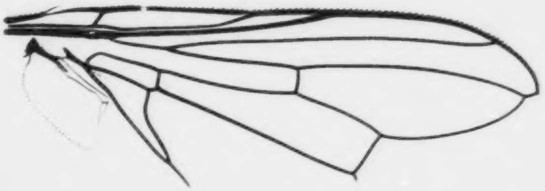
13 Ceroxys latiusculus ♀



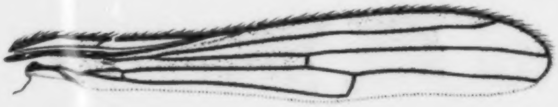
14 Psaeropterella sp. ♀



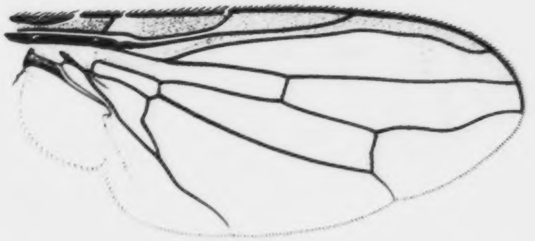
15 Stictomyia longicornis ♀



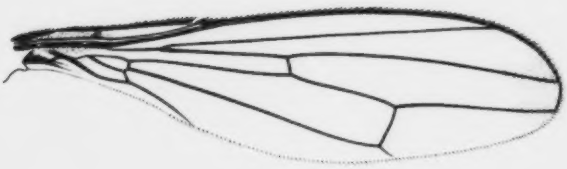
16 Physiphora aenea ♀



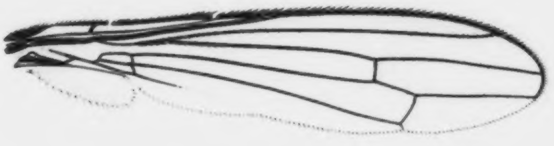
17 Steneretma laticauda ♀



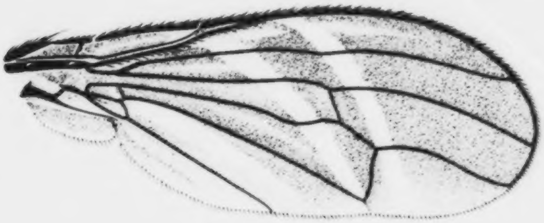
18 Notogramma cimiciforme ♂



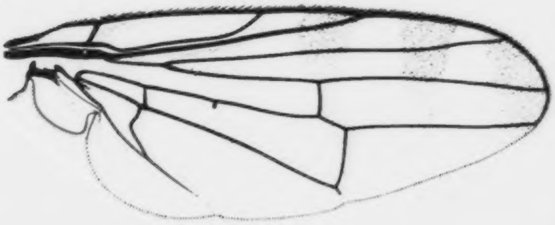
19 Myrmecothea myrmecoides ♀



20 Myiomyrmica fenestrata ♂

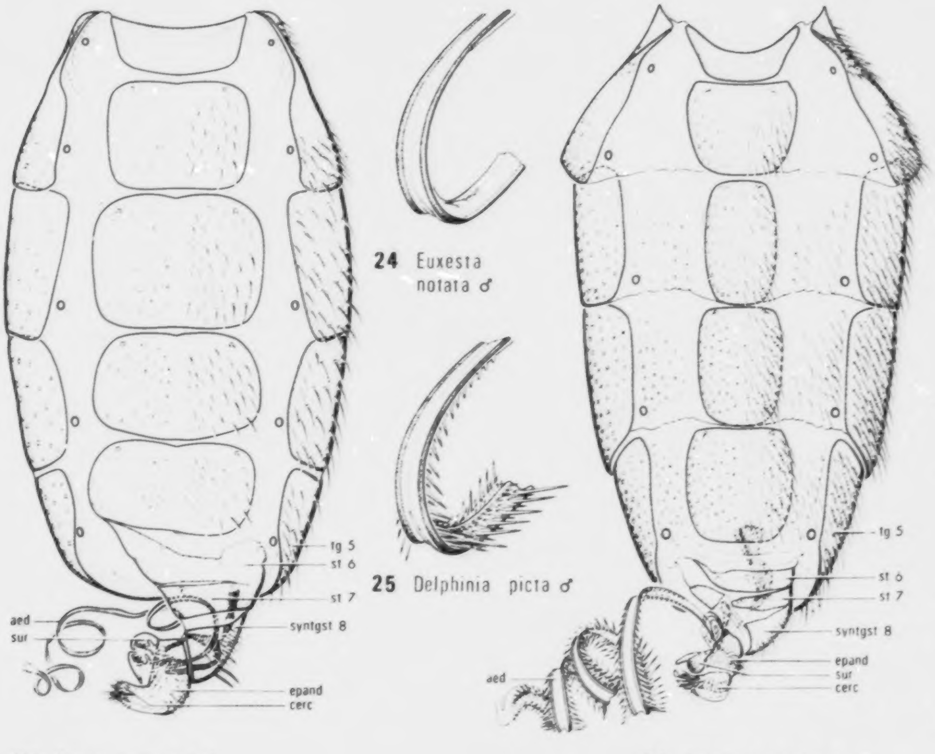


21 Tritoxa flexa ♀



22 Pseudotephritina cribellum ♀

Figs. 63.11–22. Antennae and wings: left antennae, lateral view, of (11) *Stictomyia longicornis* Bigot, (12) *Chaetopsis fulvifrons* (Macquart), (13) *Ceroxys latiusculus* (Loew), and (14) *Psaeropterella* sp.; right wings, dorsal view, of (15) *Stictomyia longicornis*, (16) *Physiphora aenea* (Fabricius), (17) *Steneretma laticauda* Loew, (18) *Notogramma cimiciforme* Loew, (19) *Myrmecothea myrmecoides* (Loew), (20) *Myiomyrmica fenestrata* (Coquillett), (21) *Tritoxa flexa* (Wiedemann), and (22) *Pseudotephritina cribellum* (Loew).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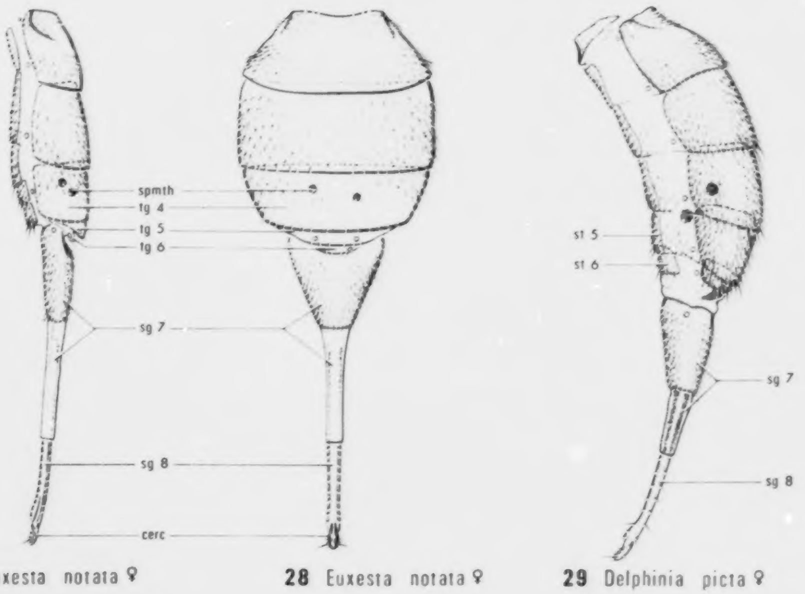
24 Euxesta notata ♂

25 Delphinia picta ♂

23 Euxesta notata ♂

26 Delphinia picta ♂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27 Euxesta notata ♀

28 Euxesta notata ♀

29 Delphinia picta ♀

Figs. 63.23–29. Abdomens and terminalia: (23) male abdomen of *Euxesta notata* (Wiedemann), ventral view; base of aedeagus of (24) *E. notata* and (25) *Delphinia picta* (Fabricius); (26) male abdomen of *D. picta*, ventral view; female abdomen of *E. notata*, (27) left lateral and (28) dorsal views, and (29) *D. picta*, left lateral view.

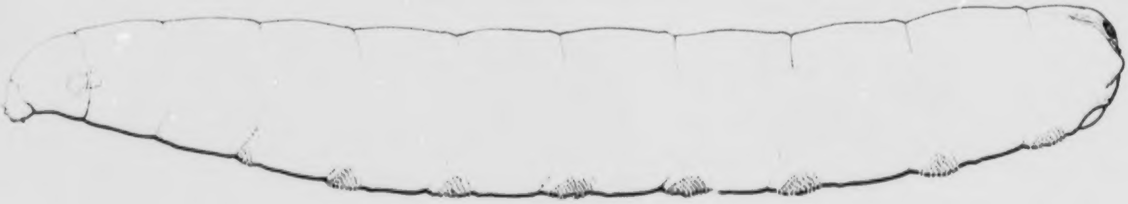
Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; sg, segment; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

5. Cell cu*p* closed apically by straight or outwardly arcuate vein, and entirely without point or extension in posteroapical corner (Fig. 21). Proepisternal bristle absent or very small 6

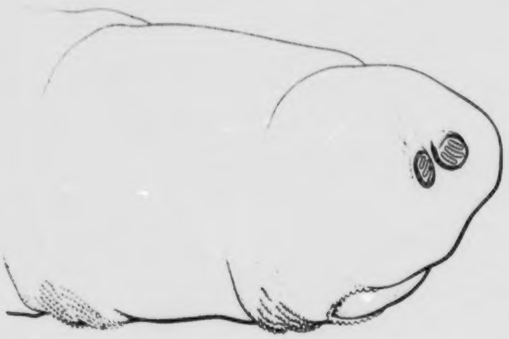
Cell cu*p* usually with at least a small point or extension in posteroapical corner (Figs. 15, 16, 18, 22). If cell cu*p* wholly without point, proepisternal bristle well-developed 13

6. R_{2+3} distinctly sinuate; R_1 setulose apically (Fig. 21). Gena not over 0.25 height of eye; eye vertically oval (Fig. 10) 7

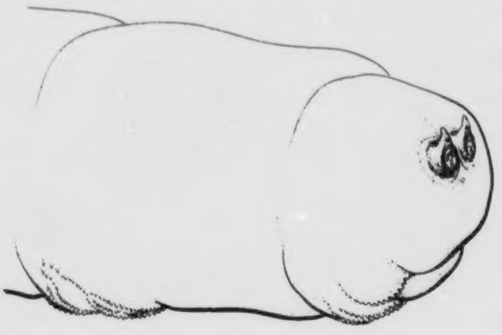
R_{2+3} straight, evenly arcuate, or slightly sinuate. If R_{2+3} sinuate, gena broader and eye roundish, or R_1 bare 8



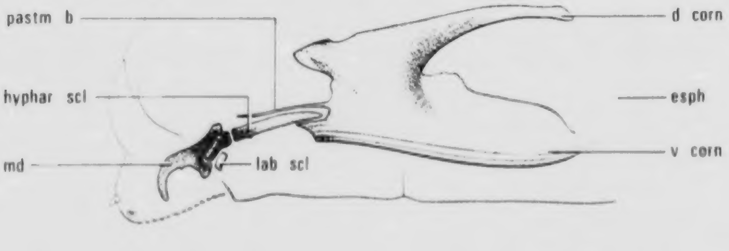
30 Pseudotephritis corticalis



31 Pseudotephritis corticalis



32 Tetanops (Eurycephalomyia) myopaeformis



33 Pseudotephritis corticalis

Figs. 63.30–33. Larvae: (30) mature larva of *Pseudotephritis corticalis* (Loew), left lateral view; enlargement of posterior end of larva of (31) *P. corticalis*, left posterolateral view, and (32) *Tetanops* (*Eurycephalomyia*) *myopaeformis* (Röder); (33) details of cephalopharyngeal skeleton of *P. corticalis*, left lateral view.

Abbreviations: d corn, dorsal cornu; esph, esophagus; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; pastm b, parastomal bar; v corn, ventral cornu.

7. Cell c wide, convex anteriorly .... ***Delphinia*** **Robineau-Desvoidy**
1 sp., *picta* (Fabricius); widespread

Cell c narrow, with anterior edge straight (Fig. 21) .... ***Tritoxa*** **Loew**
5 spp.; southern Canada to Mexico; Steyskal 1967

8. Scutellum with one pair of bristles. R_1 setulose or bare. Gena more than 0.25 height of eye; postgena swollen, shining; upper parafacial often transversely wrinkled .... ***Curranops*** **Harriot**
2 spp.; Pacific coastal regions; Steyskal 1962*b*

Scutellum with two pairs of bristles. Otherwise various 9

9. Gena less than 0.25 height of eye. Hind femur thickened, arcuate in male, with middorsal bristle. (R_1 setulose. Three dorsocentral bristles) .... ***Hiatus*** **Cresson**
1 sp., *fulvipes* Cresson; southwestern U.S.A.

Gena 0.25–0.33 height of eye. Hind femur not thickened 10

10. Frons dull. Wing without color pattern. R_1 bare or with only one or two setulae near tip .... ***Tujunga*** **Steyskal**
2 or 3 spp.; California

Frons wholly shining or dull medially. Wing with color pattern. R_1 with several setulae 11

11. Pedicel fully as long as high (Fig. 14). Frons dull medially, shining laterally .... ***Psaeropterella*** **Hendel**
2 spp.; British Columbia to California (generic status restored)

Pedicel clearly shorter than high (Fig. 7). Frons wholly shining (Fig. 7) 12

12. Crossveins r-m and dm-cu closer together than length of crossvein dm-cu. Head about as high as wide .... ***Haigia*** **Steyskal**
1 sp., *nevadana* Steyskal; Nevada to Washington and Idaho

Crossveins r-m and dm-cu widely separated. Head distinctly broader than high (Fig. 7) .... ***Homalocephala*** **Zetterstedt**
4 spp.; boreal and montane forest; Hennig 1940

13. Anepisternal bristle absent. Wing hyaline with apical brown spot 14

Anepisternal bristle present. Wing marking usually otherwise 15

14. Anepisternum with rather dense extremely fine white pile, or bare. Wing with cell r_{4+5} strongly narrowed, to no more than slightly wider at tip than length of crossvein r-m; R_1 bare .... ***Seioptera*** **Kirby**
2 spp.; widespread; Steyskal 1956, Krivosheina and Kovalev 1972

Anepisternum with short coarse blackish or dark brown setae. Cell r_{4+5} apically parallel-sided or nearly so, about twice as wide at tip as length of crossvein r-m; R_1 with at least a few setulae near tip .... ***Pseudoseioptera*** **Stackelberg**
2 spp.; central and eastern North America; Steyskal 1956 (as part of *Seioptera*)

15. R_1 bare (except in a few species of *Euxesta* in which R_{2+3} not sinuate, see couplet 28) (Figs. 15, 16, 18) 16

R_1 usually with at least a few setulae near tip; if bare, R_{2+3} sinuate 29

16. First flagellomere more than three times as long as wide (Fig. 11) 17

First flagellomere not over three times as long as wide 18

17. R_1 not nearly extending to level of crossvein r-m; pterostigmal section of C very short; wing uniformly brownish. Face protruding between antennae; gena less than 0.33 height of eye; frons with strong bristles .... ***Texasa*** **Steyskal**
1 sp., *chaetifrons* Steyskal; Texas

R_1 extending to level of crossvein r-m; pterostigmal section of C much longer than greatest width of cell c; wing with light and dark spots (Fig. 15). Face not protruding between antennae; setae of frons short and weak .... ***Stictomyia*** **Bigot**
2 spp.; southwestern U.S.A., Mexico

18. Frons pitted or strongly wrinkled (Fig. 6) 19

Frons smooth or only slightly pitted at bases of setae 20

19. Sc approaching C at a very acute angle. Disc of scutellum convex. Vertex rounded (Fig. 6) .... ***Acrosticta*** Loew

6 spp.; southern U.S.A. southward

Sc approaching C at nearly right angles (Fig. 18). Disc of scutellum flattened. Vertex acute .... ***Notogramma*** Loew

2 spp.; southern U.S.A. southward; Steyskal 1963

20. Face convex in middle; anterior margin somewhat retreating; head not longer than high (Fig. 5). Body heavily pale pruinose 21

Face straight to concave. Body not heavily pale pruinose 23

21. Wing unpatterned, not at all spotted. Face without brown to black bar or spot .... ***Ulidiotites*** Steyskal

2 or 3 spp.; noncoastal sand areas of western U.S.A.

Wing with a few dark spots anteroapically. Face with brown to black bar or spot 22

22. Crossvein dm-cu biangulate. Face with brown bar across middle (Fig. 5) ... ***Oedopa*** Loew

3 spp.; 2 spp. in western U.S.A., 1 sp. in Mexico; Steyskal 1975

Crossvein dm-cu straight. Face with central black spot .... ***Paroedopa*** Coquillett

1 sp., *punctigera* Coquillett; Arizona, New Mexico, and Texas

23. Head nearly twice as long as high; face strongly retreating (Fig. 4). Postpronotal bristle absent .... ***Eumetopiella*** Hendel

2 spp.; eastern Canada and U.S.A.

Head at most a little longer than high. Postpronotal bristle present 24

24. First flagellomere with upper apex angulate or pointed (Fig. 12). Frontal vitta bare or with a few pairs of cruciate interfrontal bristles (Fig. 3). Ovipositor broad and depressed, thin and laminar apically 25

First flagellomere usually rounded at upper apex; if this segment somewhat angulate, frontal vitta with many scattered setulae or bristles and ovipositor narrow, soft, not laminar apically 26

25. Front of head rounded in profile (Fig. 3). Posteroapical extension of cell cu*p* two or three times as long as width at base .... ***Chaetopsis*** Loew

7 spp.; widespread

Front of head angulate and produced; face distinctly retreating. Posteroapical extension of cell cu*p* scarcely longer than width at base .... ***Stenomyia*** Loew

4 described and a few undescribed spp.; widespread in east

26. Frontal vitta bare, with four low longitudinal swellings in upper part. Cell r_{4+5} closed or nearly so (Fig. 16) .... ***Physiphora*** Fallén

2 spp.; widespread; Séguy 1941 (as *Chrysomyza* Fallén)

Frontal vitta with hairs or bristles, uniformly flat throughout. Cell r_{4+5} broadly open ... 27

27. Frons 1.5 times as wide as an eye. Body in Nearctic species wholly reddish, nonmetallic. Prescutellar acrostichal bristles absent .... ***Zacompsia*** Coquillett

1 sp., *fulva* Coquillett; southeastern U.S.A.

Frons not wider than an eye. Body color more or less metallic. Prescutellar acrostichal bristles present or absent 28

28. Crossvein r-m at or beyond middle of cell dm. Prescutellar acrostichal bristles present .... ***Euxesta*** Loew

more than 30 spp.; mostly in west and south; Curran 1935

Crossvein r-m before basal one-third of cell cm. Prescutellar acrostichal bristles absent ... . ***Axiologina*** Hendel

1 sp., *ferrumequinum* Hendel; southern Florida; Steyskal 1973

29. One or more of the following characters present: pterostigmal section of C long; R_{2+3} sinuate; cell cu*p* with long extension. Proepisternal bristle small or absent 30

None of first three characters mentioned above present. Proepisternal bristle well-developed, except in *Idana*, *Tetanops*, and *Tetropismenus* 35

30. Extension of cell cu*p* much longer than $A_1 + CuA_2$. Five dorsocentral bristles present, one of which is presutural, or else only one dorsocentral bristle present, located close to scutellum. Tibiae not distinctly banded 31

Extension of cell cu*p* at most as long as $A_1 + CuA_2$ (Fig. 22). Two dorsocentral bristles present, sometimes preceded by one or two much finer setae, all postsutural. Tibiae usually distinctly banded 32

31. Five dorsocentral and five acrostichal bristles present, one of each presutural. Crossveins r-m and dm-cu parallel. Postpronotal bristle strong ....***Dyscrasis*** Aldrich

1 sp., *hendeli* Aldrich; southwestern U.S.A., Mexico

One dorsocentral and one acrostichal bristle present, both postsutural and located close to scutellum. Crossveins r-m and dm-cu strongly divergent. Postpronotal bristle weak or absent ....***Diacrita*** Gerstäcker

2 spp.; southwestern U.S.A., Mexico; Steyskal 1947

32. Scutellum laterally with pair of extensive shining black areas. Tibiae not distinctly banded, at most with lightly infuscated subbasal and apical sections 33

Scutellum wholly pruinose, gray and brown. Tibiae distinctly banded 34

33. Scutellum scarcely swollen. Frons and thorax whitish pruinose with conspicuous dark dots. Wing with transverse brown crossbands and with the anterior border alternately hyaline and brown; small stump vein projecting from M_{1+2} into cell dm (Fig. 22) ....***Pseudotephritina*** Malloch

2 spp.; central and western U.S.A.; Steyskal 1962*a*, 1974

Scutellum strongly swollen. Frons and thorax tawny, not conspicuously spotted. Wing with broad anterior border wholly yellowish to brown, without stump vein.....***Xanthacrona*** Wulp

1 sp., *bipustulata* Wulp; southern Texas; Steyskal 1966*b*

34. Anteroapical angle of cell dm close to 90°; cell dm with extensive areas of solid color; extension of cell cu*p* half or less than half as long as $A_1 + CuA_2$ ....***Pseudotephritis*** Johnson

3 spp.; widespread; Steyskal 1962*a*

Anteroapical angle of cell cu*p* about 60°; cell dm largely mottled dark brown; extension of cell cu*p* half as long or as long as $A_1 + CuA_2$ ....***Callopistromyia*** Hendel

2 spp.; widespread; Steyskal 1975

35. Gena less than 0.33 as high as eye; parafacial and fronto-orbital plate never wrinkled (Fig. 8). Two (or abnormally three) pairs of scutellar bristles present; proepisternal bristle usually well-developed, but this bristle small and weak in *Idana* and some species of *Otites* 36

Gena more than 0.33 as high as eye; parafacial and fronto-orbital plate often wrinkled (Fig. 9). Four pairs scutellar bristles sometimes present; proepisternal bristle small or absent..40

36. Frontal index (length of frons before anterior ocellus divided by narrowest width of frons, usually at level of anterior ocellus) 1.3–1.4 (Fig. 8); two dorsocentral bristles present. Size small, less than 4 mm long. (In North American species, crossveins r-m and dm-cu seldom separated by more than length of crossvein dm-cu, and with dark fascia covering both crossveins; cell cu*p* without an extension in posteroapical corner)..........***Herina*** Robineau-Desvoidy

4 spp.; widespread; McAlpine 1951

Frontal index not more than 1.2. Size larger than 4 mm 37

37. Dorsocentral bristles in five or six pairs, one pair presutural. Body pruinose. Wing with dark bars and spots ....***Melieria*** Robineau-Desvoidy

6 spp.; northward and in western mountains; Steyskal 1962*a*

Dorsocentral bristles in one or two pairs, none of which is presutural. Body and wing variable 38

38. Wing with extensive dark pattern not consisting of spots or short bars. Thorax and abdomen black, with contrasting yellow pruinose dorsal stripes .... ***Idana*** Loew

1 sp., *marginata* (Say); southeastern Canada and northeastern U.S.A.

Wing with very little pattern, or patterned with spots and short bars. Dorsum of thorax without contrasting pattern 39

39. Wing pattern at most with one short band and apical spot, or with subbasal spot only. First flagellomere rounded or slightly angulate apically .... ***Otites*** Latreille

7 spp.; central, western; Steyskal 1966*a*

Wing with six spots and short bars, including one over each crossvein (Fig. 1). First flagellomere curved and claw-like, with a sharply pointed tip (Fig. 13) .... ***Ceroxys*** Macquart

1 sp., *latiusculus* (Loew); western North America, immigrant in several other regions

40. Scutellum with three or four pairs of bristles; all bristles long. Fronto-orbital plate smooth. First flagellomere nearly circular in profile .... ***Tetropismenus*** Loew

1 sp., *hirtus* Loew; California

Scutellum with two (or abnormally three) pairs of bristles; all bristles short, inconspicuous. Fronto-orbital plate usually with one or more grooves opposite antennae (Fig. 9). First flagellomere at least 1.5 times as long as wide in profile (Fig. 9) .... ***Tetanops*** Fallén 41

41. Frons wholly shining, usually distinctly wrinkled medially and along fronto-orbital plates (Fig. 9) .... ***Tetanops*** (***Eurycephalomyia*** Hendel)

1 sp., *myopaeformis* (Röder), the sugarbeet root maggot; British Columbia to California, east to Manitoba

Frons pruinose, at least posterolaterally, with round bare spots .... ***Tetanops*** (***Tetanops*** Fallén)

5 spp.; central, southern, western; Steyskal 1970

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PLATYSTOMATIDAE

64

GEORGE C. STEYSKAL

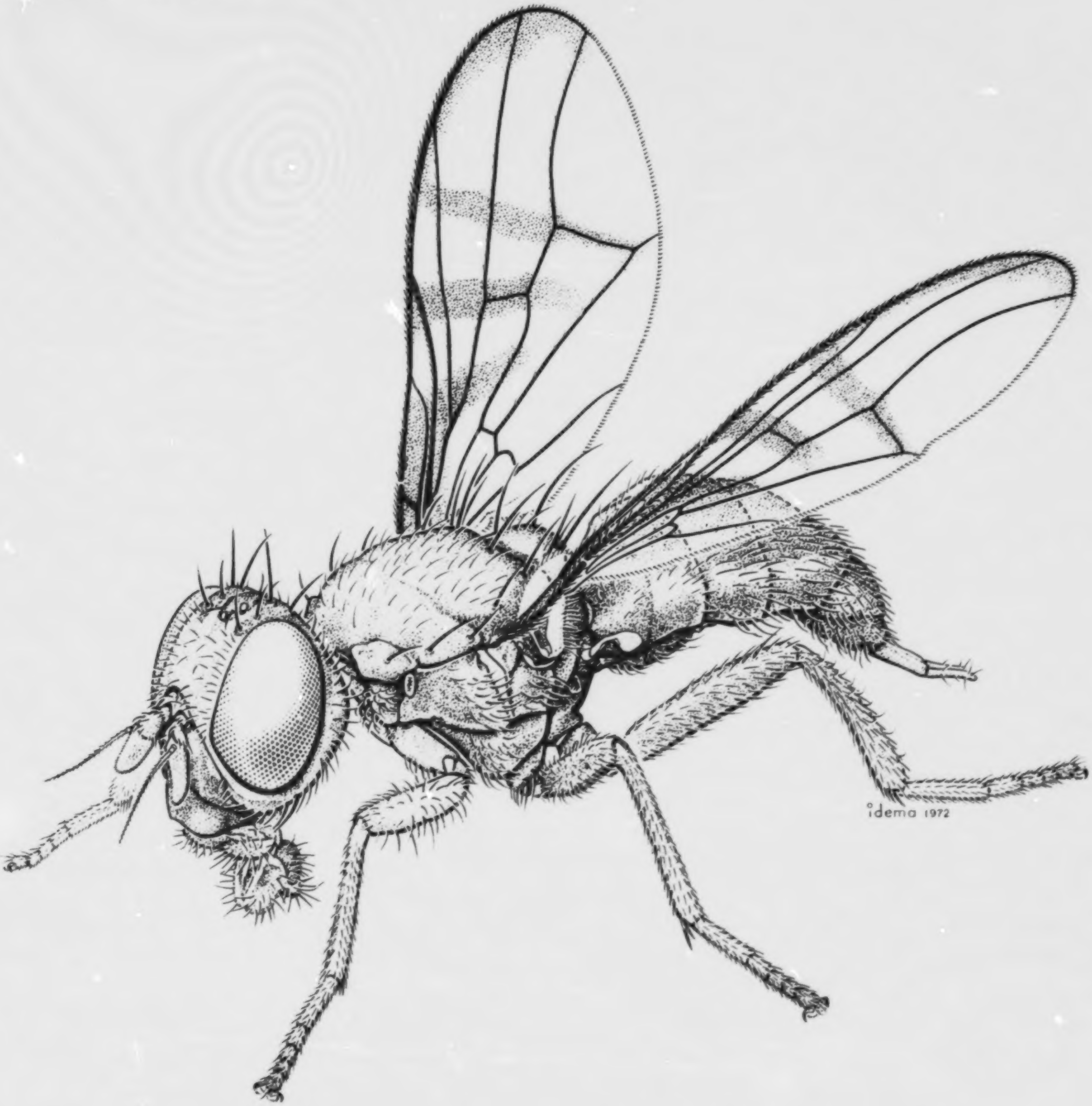


Fig. 64.1. Adult female of *Rivellia flavimana* Loew.

Flies of widely varying habitus (Fig. 1), often with bright and metallic color, and usually with strongly patterned wings. Length 3.25–12 mm.

Adult. Head: higher than long (Fig. 3). Bristles reduced in number; frontal bristles absent; only one or two orbital bristles (often very small), inner and outer vertical bristles, and one genal bristle (replaced in male of *Pogonortalis* Hendel by a group of long setae) present; ocellar and postocellar bristles reduced or lacking. First flagellomere usually long, sometimes bearing a sharp dorsoapical point; arista slender, bare to pubescent. Proboscis and palpus well-developed, but not large; palpus often broad and flattened; proboscis in some species of *Senopterina* Macquart with a pair of long slender capitate setae (Fig. 4).

Thorax: usually somewhat longer than broad. Chaetotaxy: anepisternum, anepimeron, and katepisternum setulose; katepisternal bristle absent; proepisternal bristle weak or lacking; two to four notopleural bristles present; only one postsutural pair of dorsocentral bristles present, or none at all; two or three pairs of scutellar bristles present. Wing usually rather long and narrow (Fig. 3), but short and broad in *Amphicnephes* Loew (Fig. 2); C with humeral break, without subcostal break; Sc complete, curving forward to end in C; R_1 setose dorsally; cell c*up* on upper side at least 0.25 times as long as lower side of cell dm, and never with a pointed extension on lower apex. Legs moderately developed, without conspicuous bristles.

Abdomen: varying from little longer than broad with broadest point at base to considerably longer than broad with broadest point distal of middle (Figs. 5–8), and sometimes laterally compressed; seven spiracles present in female and five in male. Terminalia of male (Fig. 9) with both inner and outer surstyli strongly developed; gonopod and paramere greatly reduced, frequently indistinguishable from hypandrium or atrophied; aedeagal apodeme fused with hypandrium; aedeagus with a slender smooth stem, and with a well-developed glans bearing a pair of sometimes very elongate apical projections; sperm pump with large ejaculatory apodeme and sclerotized cap. Female with segment 6 much shortened or absent (Figs. 5–8); terminalia with dorsoventrally flattened more or less triangular oviscape (segment 7) and with lightly sclerotized ovipositor.

Biology and behavior. Very little is known of the immature stages of Platystomatidae. No larva of any genus occurring in North America has been described. What little is known about the biology of the family in other regions (summarized by D. K. McAlpine 1973) indicates that the immature forms resemble those of the Tephritidae and Otitidae in morphology and habits.

Classification and distribution. The family is world wide in distribution but finds its greatest development in Africa, Asia, and Australia (D. K. McAlpine 1973). Most of the relatively few North American species are in the genus *Rivellia* Robineau-Desvoidy. Steyskal (1961) has given a key to genera and some data on the male terminalia. The following key is a revision of the 1961 work. The family was at one time considered a subfamily of the Otitidae.

Key to genera

1. M_1 dipping into cell dm just basal to crossvein r-m (Fig. 1). Abdomen somewhat cylindrical basally .... ***Rivellia*** Robineau-Desvoidy

34 spp. north of Mexico; also in Central America, South America, and many other parts of the world; Namba 1956

M_1 no more than slightly deflected before crossvein r-m (Figs. 2, 3). Abdomen variable 2

2. Abdomen rather broad and depressed, broadest near base (Fig. 8) 3

Abdomen somewhat compressed laterally, broadest nearer to middle (Fig. 6) 4

3. Cell bm of wing much longer than cell c*up*; no stump vein extending toward C from crossvein dm-cu; wing more than 0.4 times as wide as long (Fig. 2). Body entirely metallic blue to greenish .... ***Amphicnephes*** Loew

3 spp.: 2 spp. north of Mexico, 1 sp. extending southward to Colombia

Cell bm about equal in length to cell c*up*; stump vein present, extending toward C from crossvein dm-cu; wing somewhat less than 0.33 times as wide as long. Thorax reddish; abdomen metallic blue .... ***Himeroessa*** Loew

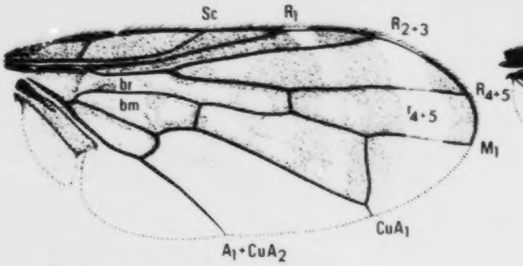
1 sp., *pretiosa* Loew; Cuba

4. Crossvein r-m oblique, beyond middle of cell dm; cell r_{4+5} parallel-sided or slightly narrowed apically (Fig. 3). Subcranial cavity ordinary (Fig. 4), without groups of long setae. Body more or less metallic blue, green, or purplish .... ***Senopterina*** Macquart

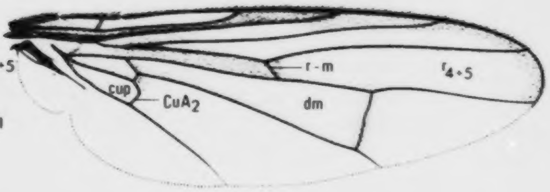
4 spp. north of Mexico, about twice as many southward (*Stenopterina*, emendation); Shewell 1962

Crossvein r-m perpendicular, before middle of cell dm; cell r_{4+5} distinctly narrowed apically. Subcranial cavity, especially in male, greatly broadened and margined laterally, with groups of long setae. Body reddish to dark brown, not metallic .... ***Pogonortalis*** Hendel

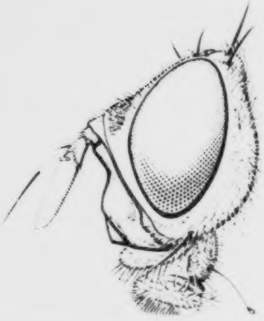
1 sp., *doclea* (Walker); immigrant in California from Australia


Sc
R1
R2+3
br
bm
R4+5
r4+5
M1
CuA1
A1+CuA2

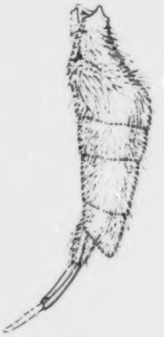
2 Amphicnephes pullus ♂


r-m
r4+5
cup
CuA2
dm

3 Senopterina caerulescens ♀



4
Senopterina
caerulescens ♀



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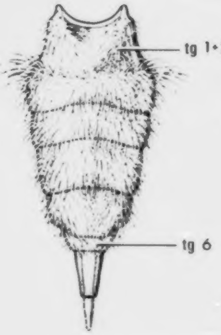

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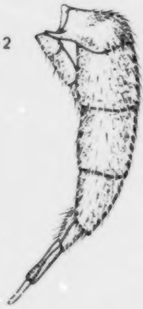
Senopterina caerulescens ♀



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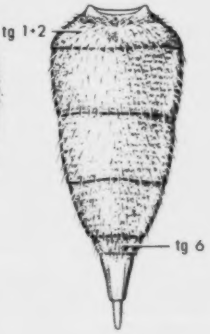
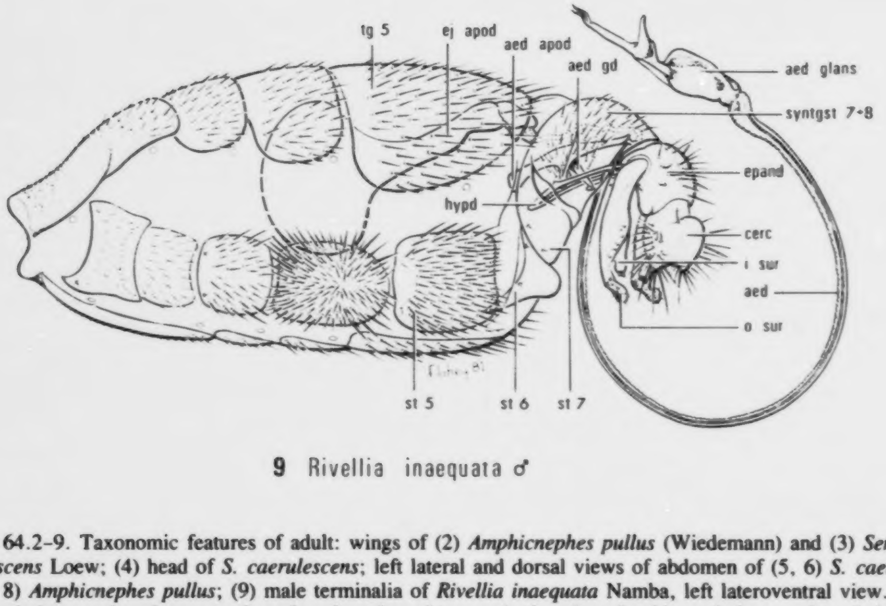


8

Amphicnephes pullus ♀


tg 5
ej apod
aed apod
aed gd
aed glans
syntgst 7+8
epand
hypd
cerc
i sur
aed
o sur
st 5
st 6
st 7

9 Rivellia inaequata ♂

Figs. 64.2–9. Taxonomic features of adult: wings of (2) *Amphicnephes pullus* (Wiedemann) and (3) *Senopterina caerulescens* Loew; (4) head of *S. caerulescens*; left lateral and dorsal views of abdomen of (5, 6) *S. caerulescens* and (7, 8) *Amphicnephes pullus*; (9) male terminalia of *Rivellia inaequata* Namba, left lateroventral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; aed glans, aedeagal glans; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; hypd, hypandrium; i sur, inner surstylus; o sur, outer surstylus; st, sternite; syntgst, syntergosternite; tg, tergite.

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PYRGOTIDAE

65

GEORGE C. STEYSKAL

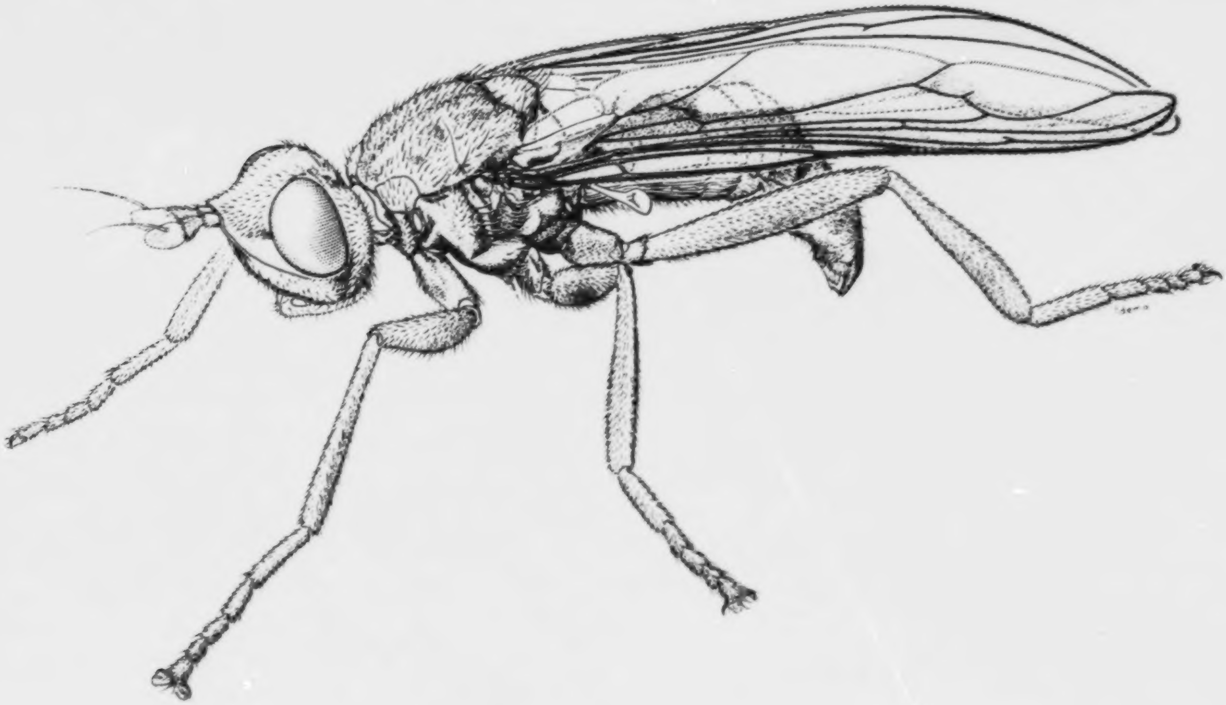


Fig. 65.1. Adult female of *Pyrgota undata* Wiedemann.

Flies moderately large, with rather slender build and rather long legs (Fig. 1). Wing 6–18 mm long, usually strongly patterned with bars, bands, or reticulation (Figs. 2–4).

Adult. Head: globose to tapering downward. Eye sometimes rather small; ocelli lacking in all North American species. Face usually rather broad, often with a strong median keel or ridge. Mouthparts of moderate size; palpus usually somewhat spatulate. Chaetotaxy variable, with reduced bristling in smaller specimens; vibrissae always lacking; all bristles somewhat reduced, but a distinct inner vertical bristle always present. Antenna rather large and porrect; pedicel usually rather elongate; first flagellomere with a bare medial or subbasal arista.

Thorax: quadrate, rather robust, not tapering forward. Chaetotaxy variable; bristles frequently weakly differentiated; basically one postpronotal, two notopleural, one supra-alar, one presutural intra-alar, two postsutural intra-alar, two postsutural dorsocentral, and one prescutellar acrostichal bristles present; all these most apparent in *Sphecomyiella* Hendel and *Boreothrinax* Steyskal. Scutellum rather short and broad, bearing up to six or seven pairs of marginal bristles or sometimes without bristles, but always setulose. Subscutellum weakly to strongly developed. Disc of proepisternum, anepisternum, katepisternum, and anepimeron always setulose, sometimes with outstanding bristles.

Wing (Figs. 2–4) elongate, with usual muscoid venation; C with humeral weakening, with or without subcostal break; Sc usually complete to C, sometimes ending beyond crossvein sc-r; R_1 setulose above; R_{2+3} frequently with preapical stump vein on posterior side (Fig. 4); cell dm long; cell r_3 widely open; cell cu*p* with lower apical corner rectangular (Fig. 3) to long and acute (Fig. 2). Alula and calypteres well-developed to nearly absent. Wing pattern in Nearctic species either with large areas of solid brown to grayish color or generally irrorate.

Legs (Fig. 1) rather long. Mid coxa unusual in lacking a mid coxal prong. Hind tibia sometimes with basal third rather suddenly smaller in diameter than apical part (Fig. 6); strong bristles lacking, even preapically; numerous fine setae often present.

Abdomen: usually elongated, in female (Fig. 8) with segment 7 sometimes longer than rest of abdomen. Terminalia of both sexes, but especially that of female, furnishing best species-diagnostic characters.

Male terminalia (Fig. 7) typical of Tephritoidea, very similar to those of Tephritidae and Platystomatidae. Aedeagal apodeme bearing lateral processes to hypandrium; aedeagus more or less coiled and elongate, with moderately specialized glans. Epandrium with more or less protruding ventral margins, more or less enclosing surstyli. Each surstylus sometimes bearing a lobate process but no prensisetae.

Female terminalia (Fig. 8) very similar to that of Tephritidae; tergite 7 and sternite 7 fused laterally, forming well-developed long conical oviscape, sometimes bearing specialized apical or subapical sensory setae, and often with special sclerotic structures such as a heavily sclerotized ventral claw that can be withdrawn. Apical segment of ovipositor small, stout, and piercing, more or less arrowhead-shaped (Figs. 8, 9), preceded by a lengthy but nearly wholly membranous tube. Two sclerotized spermathecae present in Nearctic species.

Larva and puparium. Very little is known about the morphology of pyrgotid larvae. In general, they resemble those of certain Tephritidae. Habitus figures and generalized descriptions of larva and puparium of *Pyrgota undata* Wiedemann and *Sphecomyiella valida* (Harris) were given by Davis (1919).

Biology and behavior. The Pyrgotidae are specialized for internal parasitism in the larval stages on adult scarabaeid beetles. The parasitic habit of some species may have a pronounced effect on controlling populations of pest scarabaeids. Most species of Pyrgotidae fly at night when their hosts are flying. The female deposits her eggs into the abdomen of the beetle while both are in flight.

The only data concerning American pyrgotids were presented by Forbes (1908) and Davis (1913, 1919), who reared both *Pyrgota undata* and *Sphecomyiella valida* from several species of *Phyllophaga* (Scarabaeidae, Coleoptera). One larva develops in each host. It kills the beetle in 10–14 days and pupates within the body of its host.

Classification and distribution. Three subfamilies, Lochmostyliinae, Toxurinae (see D. K. McAlpine 1978), and Pyrgotinae, are recognized. All North American genera are in the Pyrgotinae, which can be distinguished by a setiform microscopically pubescent arista and Sc meeting C at an acute angle. Within the Pyrgotinae, the Nearctic species, all Pyrgotini, are distinguished from the tribe Teretrurini, which is restricted to the Neotropical region, by the lack of ocelli and the lack of a cleft on the pedicel. The chaetotactic characters upon which many genera have been founded are unreliable because of variation in development. Characters of the terminalia have been found the most useful at all taxonomic levels.

Approximately 330 species are found in all major regions of the world, but predominantly in tropical regions. Only eight species are known at present from America north of Mexico. A synopsis of the North American species was given by Steyskal (1978).

Key to genera

1. Posterior apical corner of cell cu*p* straightly closed, forming 90° angle; alula rudimentary (Fig. 3). Face with single cup-like depression, without median keel. Body without strong bristles, even on scutellum .... ***Pyrgotella*** Curran

   1 sp., *chagnoni* (Johnson); Minnesota to North Carolina and northeastward

   Posterior apical corner of cell cu*p* angularly (Figs. 2, 4) or straightly closed, always forming much less than 90° angle; alula well-developed or absent. Face with or without median keel. Body usually with some strong bristles 2

2. Face without median keel. Alula lacking. Vein closing cell cu*p* straight, but forming acute angle with posterior side of cell cu*p*. Body without strong bristles ..... ***Stenopyrgota*** Malloch

   1 sp., *mexicana* Malloch; northward from Mexico into Arizona

   Face with median keel separating antennal grooves. Alula present. Vein closing cell cu*p* angulate. Body with strong bristles 3

3. Wing with large solid-colored areas; R_{2+3} usually with stump vein extending posteriorly at about level of crossvein dm-cu (Fig. 4). Hind tibia tapering to base (Fig. 5). Strong hook, often more or less withdrawn, near tip of abdominal sternite 7 of female .... ***Pyrgota*** Wiedemann

   2 spp.; Manitoba to Texas and eastward; Steyskal 1978

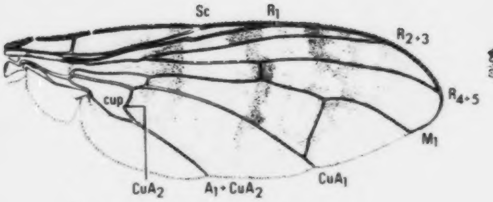
   Wing with rather finely mottled pattern; R_{2+3} without stump vein (Fig. 2). Hind tibia various. Female abdomen with or without apicoventral hook 4

4. Hind tibia tapering to base (as in Fig. 5). Ocellar and postocellar setae usually well-developed. Prosternum with lateral setae. Abdominal sternite 7 of female with strong hook at tip (Fig. 8), sometimes more or less withdrawn .... ***Sphecomyiella*** Hendel

   1 sp., *valida* (Harris); Minnesota to Arizona and eastward

   Hind tibia strongly constricted near basal third (Fig. 6). Ocellar setae usually lacking; postocellar setae always absent. Prosternum setose or bare. Abdominal sternite 7 of female without apicoventral hook .... ***Boreothrinax*** Steyskal

   3 spp.; widespread; Steyskal 1978


Sc
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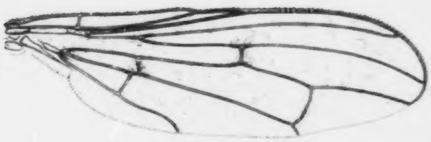
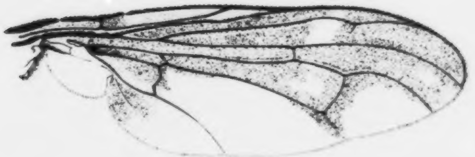
R2+3
R4+5
cup
M1
CuA2
A1+CuA2
CuA1

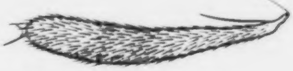
2 Sphecomyiella valida ♀



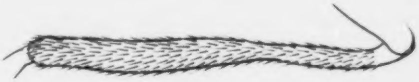
3 Pyrgotella chagnoni ♂



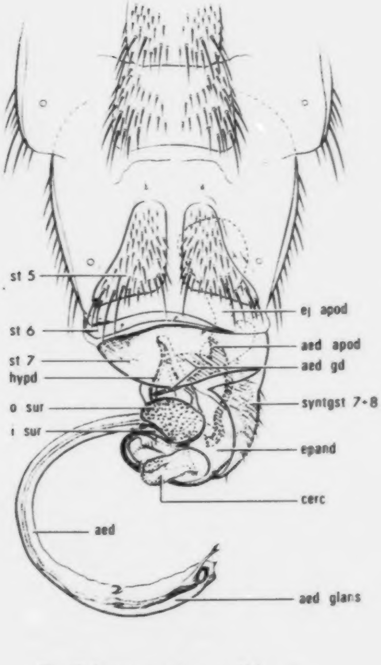
4 Pyrgota undata ♀



5 Pyrgota undata ♀



6 Boreothrinax shewelli ♀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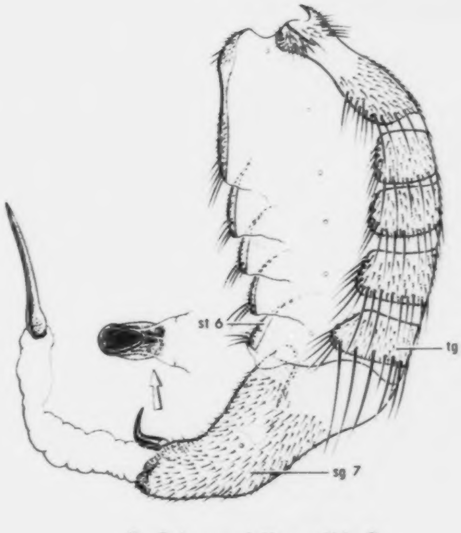
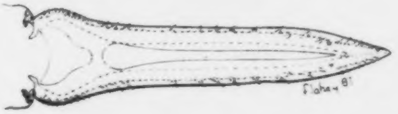
7 Sphecomyiella valida ♂



8 Sphecomyiella valida ♀



9 Sphecomyiella valida ♀

Figs. 65.2–9. Details of adult: wings of (2) *Sphecomyiella valida* (Harris), (3) *Pyrgotella chagnoni* (Johnson), and (4) *Pyrgota undata* Wiedemann; left hind tibiae of (5) *P. undata* and (6) *Boreothrinax shewelli* Steyskal; (7) male terminalia of *S. valida*, left lateral view; (8) female abdomen and terminalia of *S. valida*, left lateral view, with enlargement of specialized process of sternite 7 in ventral view; (9) sclerotized apical portion of ovipositor of *S. valida*, in dorsal view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; aed glans, aedeagal glans; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; hypd, hypandrium; i sur, inner lobe of surstylus; o sur, outer lobe of surstylus; sg, segment; st, sternite; syntgst, syntergosternite; tg, tergite.

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TEPHRITIDAE

66

RICHARD H. FOOTE AND GEORGE C. STEYSKAL

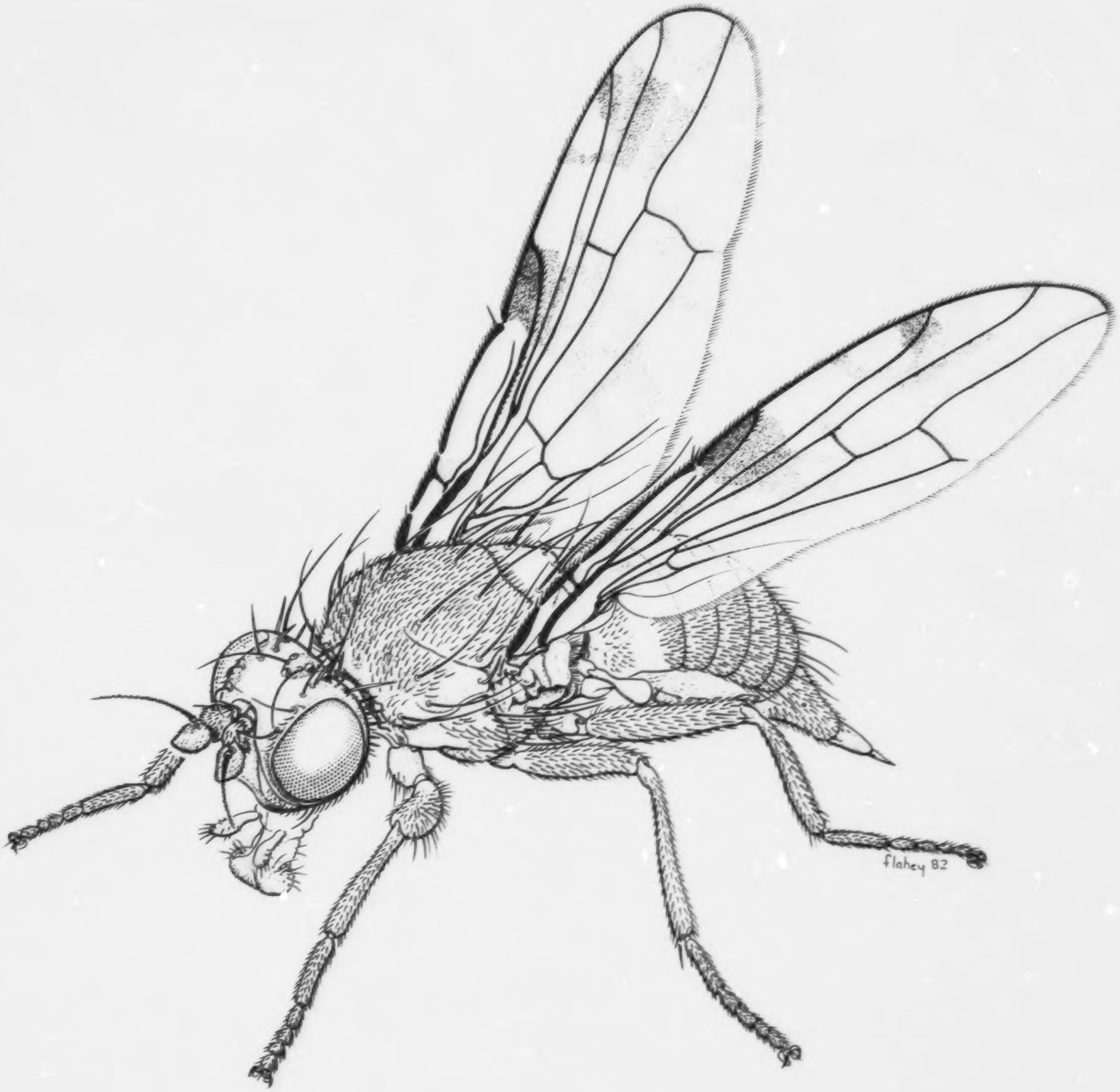

Fig. 66.1. Adult female of *Tephritis angustipennis* (Loew).

Flies varying from small to moderately large (Fig. 1). Wing usually more or less distinctly patterned, but a few species having no wing pattern at all; apical part of Sc weakened and sharply bent forward. Body variously colored, sometimes quite brightly. Larva maggot-like, living within plant tissue.

Adult. Head: widely varying in shape (Figs. 2–7). Eye stalked in a few exotic species. Chaetotaxy: usually one pair each of well-developed inner and outer vertical, divergent postocellar, and ocellar bristles present; frons with one to several pairs of orbital bristles, at least one of which is reclinate, and one to five pairs of more or less inclinate frontal bristles; some bristles often thickened, flattened, blunt-ended, or white; sometimes, as in male of Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), one pair of orbital bristles elongated and bearing a flattened expansion at or near tip; and sometimes, as in male of *Strauzia longipennis* (Wiedemann) (Fig. 5), one or more pairs of frontal bristles enlarged and flattened; vibrissae absent, although in a few genera sometimes simulated by subvibrissal or genal bristles. Antenna simple; pedicel usually with a dorsal seam, much as in Calyptratae; first flagellomere frequently with a sharply pointed dorsal apex (Fig. 2); arista usually bare or shortly haired. Proboscis and palpus well-developed; proboscis sometimes long and reflexed (Fig. 3).

Thorax: variable in shape and size. Scutellum swollen and shiny in several genera. Chaetotaxy: very important taxonomically; most bristles found in muscoid Diptera present in one or another genus (Figs. 8–11); bristles, however, frequently rather inconspicuous; scutum always with at least two conspicuous bristles designated dorsocentral and acrostichal setae (Figs. 8–11); a typical proepisternal bristle always lacking; proepimeron always with one or more bristles or hairs; anepisternum, katepisternum, and anepimeron always with bristles or hairs, or both; one to four pairs of scutellar bristles present, nearly always marginal.

Wing always well-developed, varying greatly in shape, with typical muscoid venation (Figs. 12–37). Sc distinctively turned sharply toward C and greatly weakened beyond the bend. R_1 always setulose above. Posterior apex of cell cu*p* usually more or less extended; cell cu*p* in a few genera closed apically by a straight or evenly convex vein (Fig. 14); cell r_{4+5} sometimes with a thickened and darkened bulla in membrane (Figs. 26, 28). Color pattern usually present to varying degrees, from almost wholly blackish to varying combinations of bands, stripes, spots, or reticulation, usually highly species-diagnostic, sometimes differing between sexes, sometimes lacking. Extent and kind of vestiture also sometimes differing considerably between sexes.

Legs usually unmodified, with reduced bristling. True dorsal preapical tibial bristles lacking; frequently a row of median anterodorsal bristles present on hind tibia; median posterodorsal bristles present on middle tibia. Anterior femur usually with rows of well-developed dorsal and ventral bristles; middle and hind femora usually bearing few or no distinct bristles.

Abdomen: varying from long and cylindrical to short and triangular or stubby (Figs. 38, 39, 42).

Terminalia of male twisted at rest, stowed between tergite 5 and sternite 5 in right side of abdomen (Figs. 38–40). Epandrium (Fig. 41) bearing a pair of more or less elongated posteroventral surstyli; a pair of stout, usually black, toothlike prensisetae present on medial side of each surstylus. Aedeagus long and tubular, coiled at rest, bearing a usually complex glans at its tip (Fig. 41).

Female terminalia (Figs. 42–44) very short to very long; segment 7 forming a more or less conical, frequently dorsoventrally flattened basal oviscape (ovipositor sheath, oviscapt) derived from laterally fused tergite 7 and sternite 7, and containing spiracle 7 on each side. Segment 8 comprising main shaft of a strongly sclerotized ovipositor which, at rest, lies telescoped within a very tough, membranous, eversible ovipositor sheath (ovipositubus). Eversible ovipositor sheath derived anteriorly from segment 7 and posteriorly from intersegmental membrane between segments 7 and 8, with a dorsal and a ventral pair of strips of more strongly sclerotized but still flexible cuticle extending from posterior margins of tergite 7 and sternite 7; distal part of ovipositor sheath with a rasper composed of recurved spicules or densely sclerotized teeth. Cerci fused and typically pointed to serve as a piercing organ at apex of ovipositor; lateral serrations sometimes present; a pair of preapical ventral flaps, formed from apices of a divided sternite 8, more or less enclosing genital opening, through which egg is extruded. Two or three variously shaped spermathecae present, sometimes heavily sclerotized.

Larva. Typical maggots. Body varying from quite elongate to very short and thick; color white, yellowish, or brown; posterior end of lighter colored species sometimes black. Two mandibles present, sometimes furnished with teeth along ventral margin; antennomaxillary lobes at each side of mandibles with several transverse oral ridges or backwardly directed short laminae. Anterior spiracles ending bluntly, not elongated, and each with as few as three openings or up to more than 50 arranged either transversely in one to three groups or irregularly. Each posterior spiracle without a clearly defined peritreme; each with three spiracular openings in mature larvae, usually more or less horizontal and parallel to each other, and usually accom-

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Figs. 66.2–7. Heads: (2) *Rhagoletis pomonella* (Walsh), anterior view; (3) *Dioxyna picciola* (Bigot), left lateral view; left anterolateral views of (4) *Chaetostomella undosa* (Coquillett), (5) male and (6) female of *Strauzia longipennis* (Wiedemann), and (7) *Gymnocarena diffusa* (Snow).

Abbreviations: ar, arista; clyp, clypeus; fc, face; fc car, facial carina; flgm, flagellomere; fr s, frontal seta; gn s, genal seta; i vt s, inner vertical seta; lun, lunule; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; plp, palpus; poc s, postocellar seta; sbvb s, subvibrissal seta.

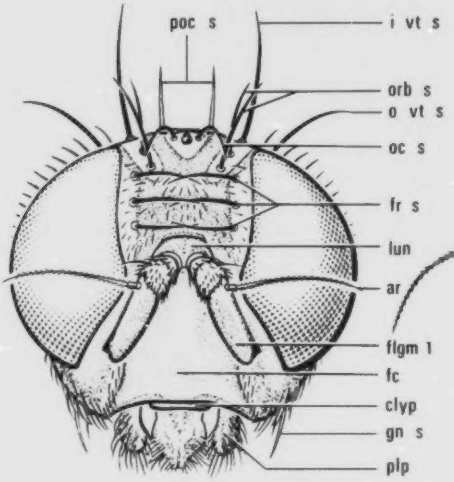
⇨

panied by branched spiracular hairs in four tufts (Fig. 5.105). Details of many species described and illustrated by Phillips (1946). Puparium remaining colorless, or in some species becoming quite black.

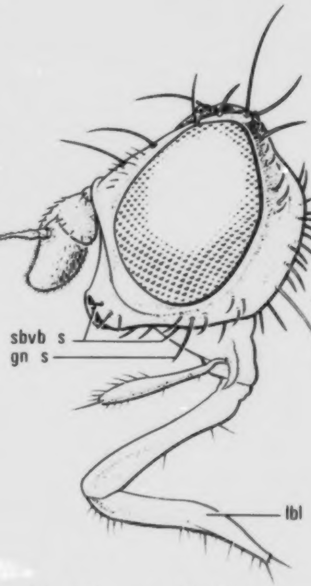
Biology and behavior. All tephritid larvae feed upon living plant tissue, in which the eggs are laid. Every part of the plant structure is utilized by one or another species, and many species form galls. Wasbauer (1972) has listed the hosts of North American Tephritidae and has included an extensive bibliography. All hosts are dicotyledonous seed plants except *Juniperus* (Cupressaceae; gymnospermous), *Poa* (Gramineae; monocotyledonous), and *Musa* (Musaceae, monocotyledonous). The Asteraceae (=Compositae) are a preferred family. The biology of the Tephritidae was reviewed by Christenson and Foote (1960). Many species are economically important either as pests of useful plants or as control agents for weeds.

Classification and distribution. The Tephritidae are one of the largest families of Diptera. About 4000 species are found throughout the world, but the number of species is greatest in tropical regions.

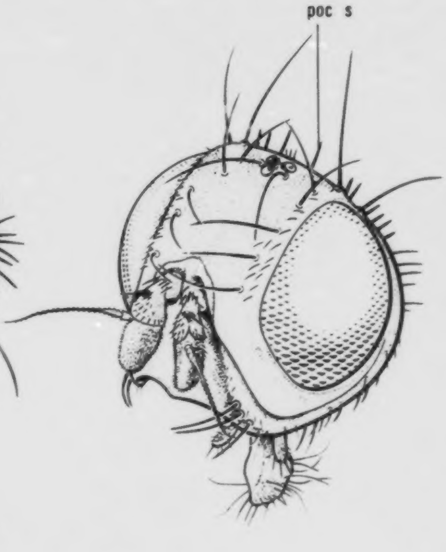
Major changes in the classification of the Tephritidae have been made in the past few decades. The last comprehensive review of the family for North America (Phillips 1923) is now seriously out of date, although still useful. The species of the southeastern United States are treated by Benjamin (1934), and those of California by Foote and Blanc (1963).



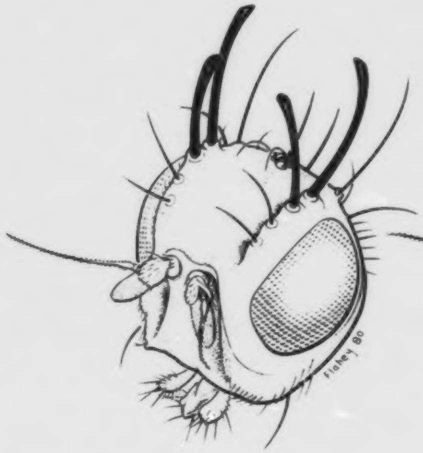
2 Rhagoletis pomonella ♀



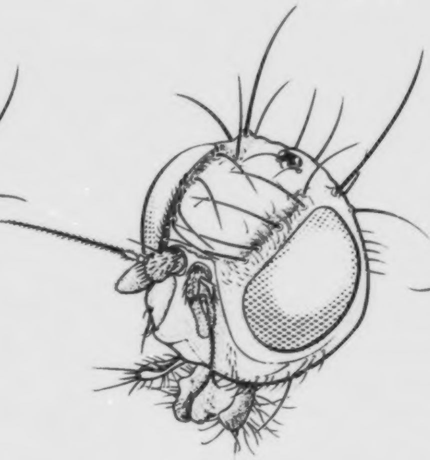
3 Dioxyna picciola ♀



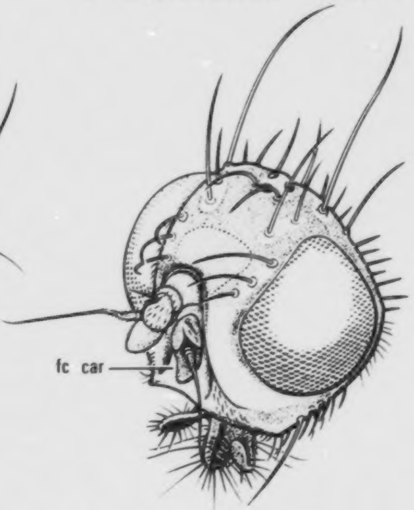
4 Chaetostomella undosa ♀



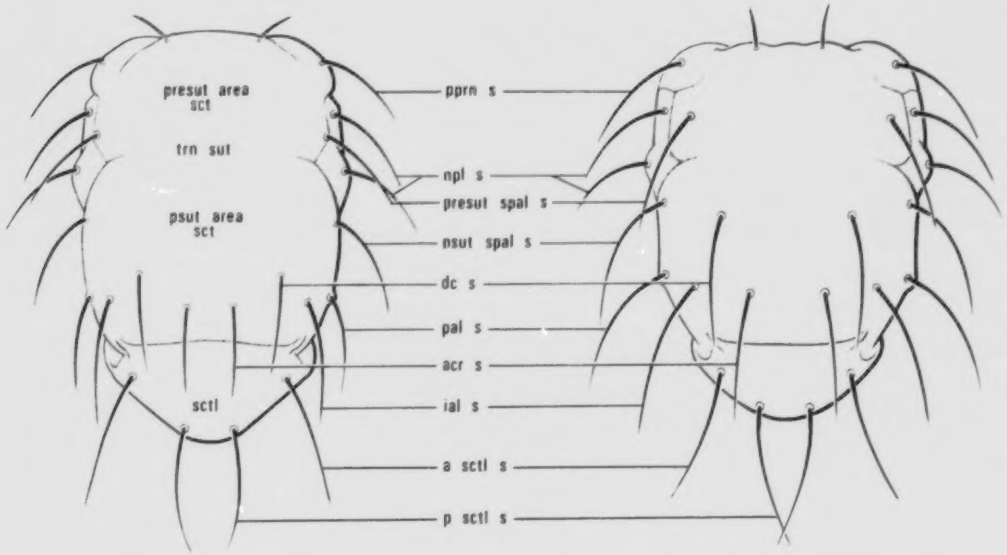
5 Strauzia longipennis ♂



6 Strauzia longipennis ♀



7 Gymnocarena diffusa ♂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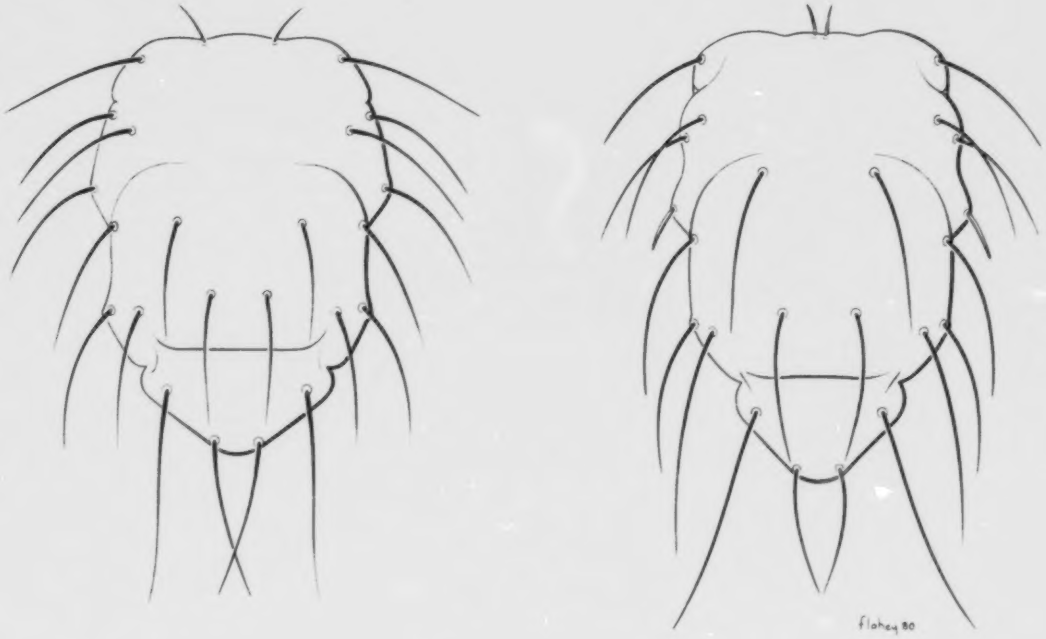
8 Anastrepha ludens ♀ **9** Rhagoletis pomonella ♀



10 Strauzia longipennis ♀ **11** Neotephritis finalis ♀

Figs. 66.8–11. Dorsal thoracic chaetotaxy: (8) *Anastrepha ludens* (Loew); (9) *Rhagoletis pomonella* (Walsh); (10) *Strauzia longipennis* (Wiedemann); (11) *Neotephritis finalis* (Loew).

Abbreviations: a, anterior; acr, acrostichal; dc, dorsocentral; ial, intra-alar; npl, notopleural; p, posterior; pal, postalar; pprn, postpronotal; presut, presutural; psut, postsutural; s, seta or bristle; sct, scutum; sctl, scutellum; spal, supra-alar; trn sut, transverse suture.

Generic revisions that have appeared in recent years are referred to in the following key, but work on several genera is still needed.

The North American genera can no longer be distinctly divided into the two subfamilies Tephritinae and Trypetinae. Hering (1947) proposed a revision in which eight subfamilies and 17 tribes are recognized, but many exceptions are cited and the distinctions between the groups are not clear. In the present treatment only two genera (*Dacus* Fabricius and *Toxotrypana* Gerstäcker) are placed in the Dacinae, and two (*Rhynencina* Johnson and *Urophora* Robineau-Desvoidy) in the Myopitinae (=Euribiinae, Urophorinae). The remainder are considered as Tephritinae, which will eventually be divisible into several tribes. However, the classification into tribes (or possibly other subfamilies) is still unsettled and must be worked out on a world basis to be realistic.

Two genera, *Tetreuaresta* Hendel and *Ensina* Robineau-Desvoidy, not at present known to occur in North America, are included in the key because they will likely eventually be found there. *Ceratitis* Macleay and *Dacus* are included because they have been previously introduced.

Many species are difficult to recognize in the larval stage because the larvae of species belonging to genera in different subfamilies appear nearly indistinguishable. Keys to the larvae therefore must be constructed largely species by species, as is the one by Phillips (1946), the only comprehensive treatment of North American tephritid larvae that has been published.

Key to genera

1. Postpronotal, dorsocentral, katepisternal, and ocellar bristles absent ...... DACINAE 2

One or more of above pairs of bristles always present 3

2. Cell bm much wider than cell cu*p*; R_{2+3} not undulate and without appendix (Fig. 12). Oviscape much shorter than preceding portion of abdomen ...... ***Dacus*** Fabricius

1 sp., *dorsalis* Hendel; immigrant in California; many species, worldwide

Cell bm and cell cu*p* approximately equal in width; R_{2+3} undulate, with at least one short appendix (Fig. 13). Oviscape longer than preceding portion of abdomen ...... ***Toxotrypana*** Gerstäcker

1 sp., *curvicauda* Gerstäcker; southern Florida and Texas southward; Benjamin 1934

3. Apex of cell cu*p* closed by transverse or slightly convexly bent vein; posteroapical corner never drawn out into a point (Fig. 14) ...... MYOPITINAE 4

Apex of cell cu*p* closed by concavely bent vein; posteroapical corner drawn out into a point (Figs. 15–37) ...... TEPHRITINAE 5

4. Lower margin of face strongly produced. Proboscis strongly geniculate; labella slender and longer than head ...... ***Rhynencina*** Johnson

1 sp., *longirostris* Johnson; Pennsylvania to Georgia

Lower margin of face not strongly produced. Proboscis at most shortly geniculate ...... ***Urophora*** Robineau-Desvoidy

5 spp. native in western U.S.A., together with a few Palaearctic species introduced for weed control; Steyskal 1979

5. Dorsocentral bristles not arising farther forward than midpoint between supra-alar and acrostichal bristles (Fig. 8), or if so, upper orbital bristles reclinate (Fig. 4) and wing with dark bands over crossveins r-m and dm-cu, forming a V that encloses a small dark costal spot (Fig. 16) 6

Dorsocentral bristles arising anterior to midpoint between supra-alar and acrostichal bristles (Figs. 9–11), except in some species of *Myoleja* 10

6. M curved forward apically; wing pattern normally as in Fig. 15 ...... ***Anastrepha*** Schiner

20 spp., Florida, southern Texas; many others southward; Stone 1939*a*, 1939*b*, 1942; Shaw 1962; Steyskal 1977*a*, 1977*b*

M not curved forward apically 7

7. Scutellum with three or more pairs of setae ...... ***Hexachaeta*** Loew

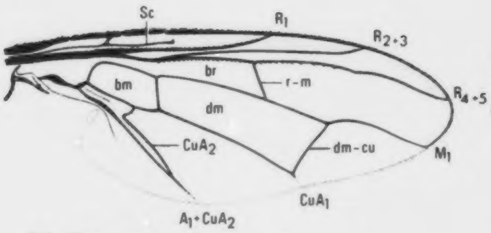
3 spp.; Texas; Foote 1967

Scutellum with no more than two pairs of setae 8

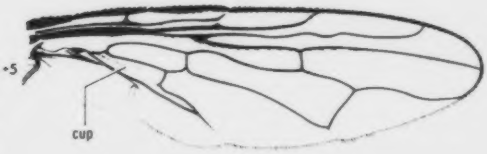
8. Upper orbital bristles convergent ...... ***Paraterellia*** Foote

4 spp.; western U.S.A.; Foote 1960*a*, Foote and Blanc 1979

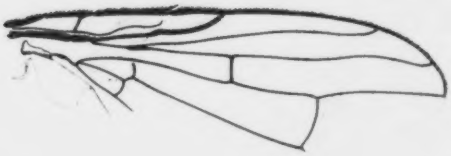
Upper orbital bristles divergent, reclinate, or absent 9



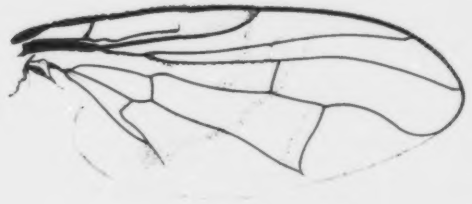
12 Dacus dorsalis ♀



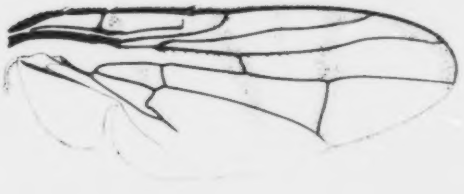
13 Toxotrypana curvicauda ♀



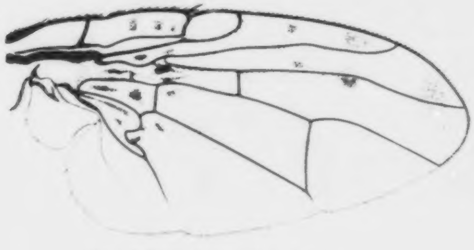
14 Urophora jaceana ♀



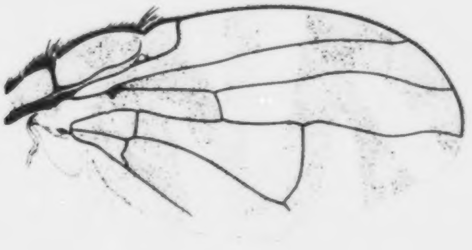
15 Anastrepha ludens ♀



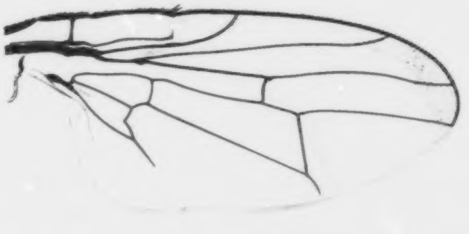
16 Zonosemata vittigera ♀



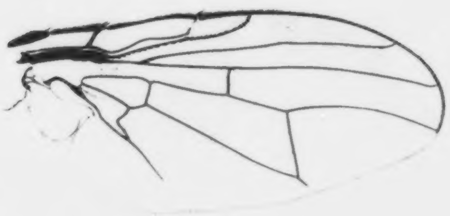
17 Ceratitis capitata ♀



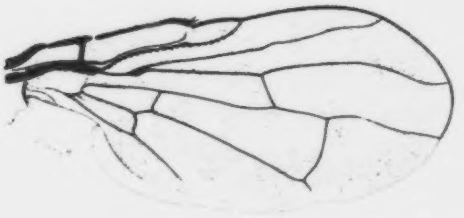
18 Stenopa vulnerata ♀



19 Procecidocharoides penelope ♀

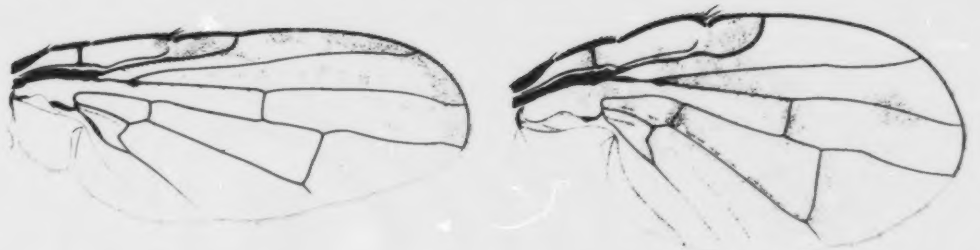


20 Rhagoletis pomonella ♂



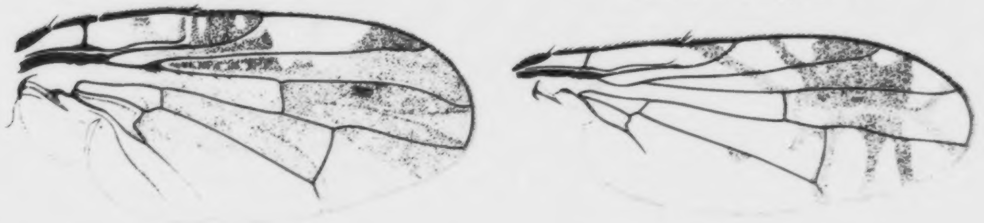
21 Eurosta comma ♀

Figs. 66.12–21. Wings: (12) *Dacus dorsalis* Hendel; (13) *Toxotrypana curvicauda* Gerstäcker; (14) *Urophora jaceana* (Hering); (15) *Anastrepha ludens* (Loew); (16) *Zonosemata vittigera* (Coquillett); (17) *Ceratitis capitata* (Wiedemann); (18) *Stenopa vulnerata* (Loew); (19) *Procecidocharoides penelope* (Osten Sacken); (20) *Rhagoletis pomonella* (Walsh); (21) *Eurosta comma* (Wiedemann) (*continued*).



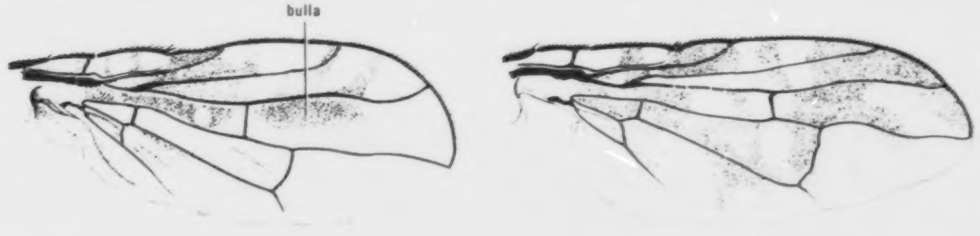
22 Icterica seriata ♀

23 Xanthomyia platyptera ♂



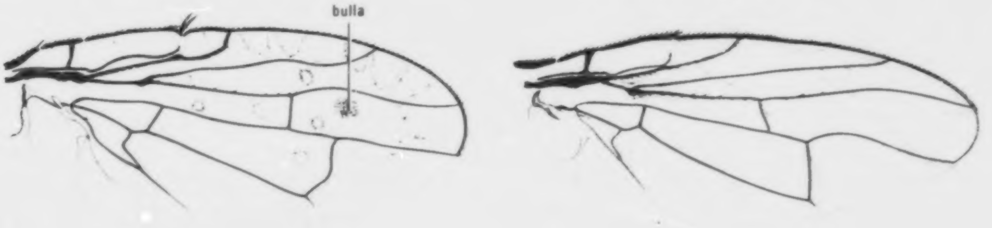
24 Jamesomyia geminata ♀

25 Trupanea actinobola ♀



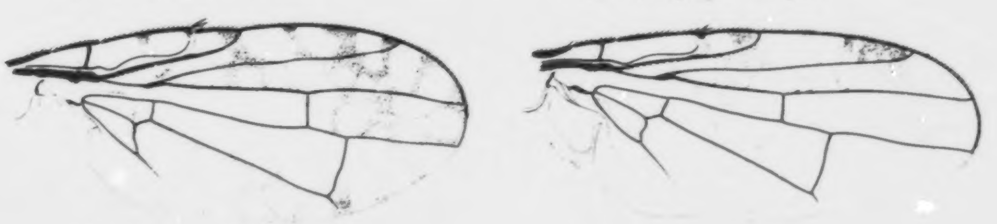
26 Valentibulla californica ♀

27 Aciurina bigeloviae ♀



28 Paracantha culta ♂

29 Tomoplagia obliqua ♀



30 Euaresta aequalis ♂

31 Acinia picturata ♀

Figs. 66.22–31. Wings (*continued*): (22) *Icterica seriata* (Loew); (23) *Xanthomyia platyptera* (Loew); (24) *Jamesomyia geminata* (Loew); (25) *Trupanea actinobola* (Loew); (26) *Valentibulla californica* (Coquillett); (27) *Aciurina bigeloviae* (Cockerell); (28) *Paracantha culta* (Wiedemann); (29) *Tomoplagia obliqua* (Say); (30) *Euaresta aequalis* (Loew); (31) *Acinia picturata* (Snow) (*continued*).

9. Apical one-third of mid and hind femora with small ventral spines. First flagellomere rounded apically . . . . ***Oedicarena*** Loew

2 spp.; western and central U.S.A.; Steyskal and Foote 1977

Mid and hind femora without such spines. First flagellomere acute apically . . . . ***Zonosemata*** Benjamin

2 spp.; eastern and central U.S.A.; Bush 1965

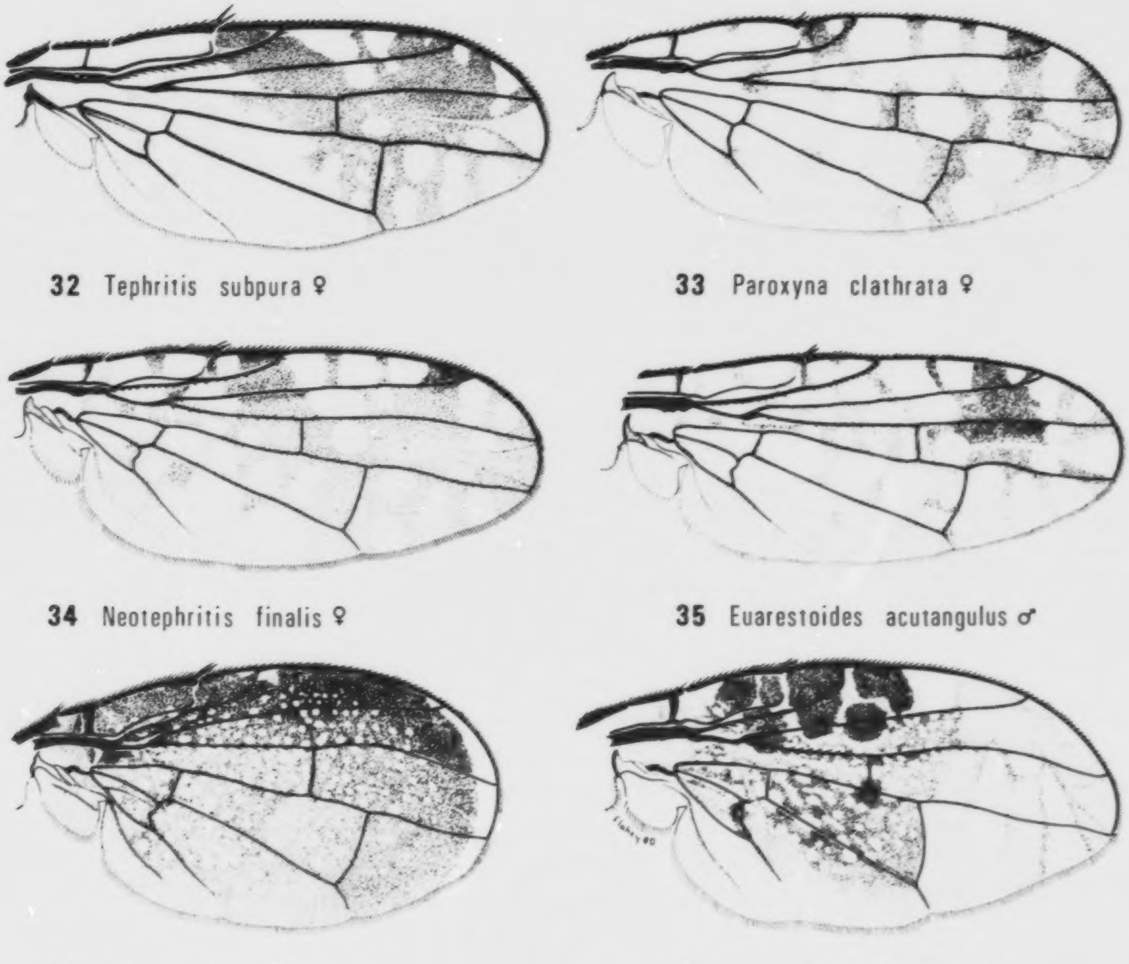
10. Scutellum inflated, usually polished or bilobate. Wing with dark bands on hyaline background; pattern not reticulate 11

Scutellum not distinctly swollen or polished. Wing sometimes with reticulate pattern 17

11. Lower outer corners of face with white setae. Wing with a supernumerary crossvein between apices of R_1 and R_{2+3} . . . . ***Callachna*** Aldrich

1 sp., *gibba* (Loew); eastern U.S.A., Texas; Aldrich 1929

Lower outer corners of face without white setae. Wing without a supernumerary crossvein between apices of R_1 and R_{2+3} 12



32 Tephritis subpura ♀

33 Paroxyna clathrata ♀

34 Neotephritis finalis ♀

35 Euarestoides acutangulus ♂

36 Eutreta frontalis ♀

37 Acrotaenia testudinea ♀

Figs. 66.32–37. Wings (*concluded*): (32) *Tephritis subpura* (Johnson); (33) *Paroxyna clathrata* (Loew); (34) *Neotephritis finalis* (Loew); (35) *Euarestoides acutangulus* (Thomson); (36) *Eutreta frontalis* Curran; (37) *Acrotaenia testudinea* (Loew).

12. Wing proximal to subcostal break patterned with dark streaks and spots in middle of cells; posteroapical extension of cell cu*p* expanded (Fig. 17). Male with lower orbital bristle spatulate apically . . . . ***Ceratitis*** Macleay

1 sp., Mediterranean fruit fly, *capitata* (Wiedemann); adventive in Florida, Texas, and California, and still an ominous threat

Wing with dark color proximal to subcostal break, not patterned with streaks and spots in middle of cells; posteroapical extension of cell cu*p* cuneate (Figs. 18, 19). Orbital bristles simple 13

13. Scutellum bilobate, with shallow median depression dorsally . . . . ***Peronyma*** Loew

1 sp., *sarcinata* (Loew); southeastern U.S.A.

Scutellum evenly rounded dorsally 14

14. Crossvein r-m near middle of cell dm, not in same dark band that covers crossvein dm-cu (Fig. 18) 15

Crossvein r-m well distal of middle of cell dm, in same dark band that covers crossvein dm-cu (Fig. 19) 16

15. Wing with transverse hyaline band between crossveins r-m and dm-cu not extending any further posteriorly than cell dm (Fig. 18). Anepimeron black . . . . ***Stenopa*** Loew

2 spp.; widespread; Quisenberry 1949*b*

Wing with transverse hyaline band between crossveins r-m and dm-cu extending to posterior margin. Anepimeron inflated, whitish . . . . ***Cecidocharella*** Hendel

1 sp., *borrichia* Bush & Huettel; Texas; Bush and Huettel 1970

16. Two pairs of well-developed orbital bristles present; posterior pair convergent. Hyaline area between second and third wing bands with dark mark posterior to middle of cell dm (Fig. 19) . . . . ***Procecidocharoides*** Foote

4 spp.; widespread; Foote 1960*c*

One or two pairs of orbital bristles present; posterior pair, if present, minute and more or less divergent. Hyaline area between second and third wing bands without a dark mark . . . . ***Procecidochares*** Hendel

12 spp.; widespread; Aldrich 1929

17. Upper orbital bristles strongly convergent (Fig. 4) 18

Upper orbital bristles reclinate (Figs. 5–7) or absent 20

18. Anteroventral margin of gena with a few well-developed subvibrissal bristles larger than adjacent setulae (Fig. 4) . . . . ***Chaetostomella*** Hendel

1 sp., *undosa* (Coquillett); western; Steyskal and Foote 1977

Anteroventral margin of gena with only uniformly small subvibrissal setulae 19

19. Node of Rs with one to several setae dorsally. Palpus usually conspicuously projecting beyond lower margin of face . . . . ***Orellia*** Robineau-Desvoidy

3 spp.; widespread; McFadden and Foote 1961

Node of Rs without setae. Palpus never projecting beyond lower margin of face . . . . ***Neaspilota*** Osten Sacken

11 spp.; widespread; Malloch 1942, Quisenberry 1949*b*

20. Dorsocentral bristles closer to level of supra-alar bristles than to transverse suture (Fig. 10) 21

Dorsocentral bristles closer to transverse suture than to level of supra-alar bristles (Fig. 11); if doubtful, dark bulla present in cell r_{4+5} (Figs. 26, 28) 37

21. Lower margin of gena with several well-developed subvibrissal bristles anterior to genal bristle . . . . ***Chetostoma*** Rondani

2 spp.; western U.S.A.; Blanc 1959

Lower margin of gena without strong subvibrissal bristles anterior to genal bristles 22

22. At most, with only one pair of orbital bristles (Figs. 5, 6) 23

Two to four pairs of orbital bristles present (Figs. 2, 7) 25

23. Presutural supra-alar bristle absent. Antenna extending to or nearly to lower margin of face ...... ***Epochra*** Loew

1 sp., *canadensis* (Loew); south to California and New York

Presutural supra-alar bristle present (Fig. 10). Antenna extending slightly below middle of face (Figs. 5, 6) 24

24. Head higher than long, rounded below. Proboscis not geniculate (Figs.5, 6). Wing with pronounced banded pattern ...... ***Strauzia*** Robineau-Desvoidy

1 sp., *longipennis* (Wiedemann); absent from west coast of North America

Head longer than high, straight below. Proboscis geniculate (as in Fig. 3). Wing pattern nearly absent or consisting of a few spots ...... ***Ensina*** Robineau-Desvoidy

1 sp., *sonchi* Robineau-Desvoidy; nearly cosmopolitan and may eventually be found in North America

25. Crossvein r-m approximately at middle of cell dm (Fig. 20) 26

Crossvein r-m distinctly distal of middle of cell dm (Figs. 21–24), rather close to crossvein dm-cu 28

26. First flagellomere pointed at upper apex (Fig. 2) ...... ***Rhagoletis*** Loew

21 spp.; widespread; Bush 1966

First flagellomere rounded apically (as in Figs. 3, 5–7) 27

27. Background color of body yellow, sometimes with a few dark markings ...... ***Trypeta*** Meigen

7 spp.; widespread, mostly in north; Foote 1960*b*

Background color of body dark brown to black, with a yellowish median streak on scutum ...... ***Rhagoletotrypeta*** Aczél

2 spp.; northeastern U.S.A., Texas; Steyskal 1981

28. All postocular bristles black 29

Some postocular bristles whitish or yellowish 30

29. Facial carina strongly developed, protuberant. Posterior part of thorax in dried specimens usually speckled with black dots ...... ***Euleia*** Walker

2 spp.; widespread; Foote 1959

Facial carina not strongly developed. Thorax without black dots ...... ***Myoleja*** Rondani

4 spp.; 3 spp. from eastern North America and 1 sp. from Pacific Coast; Steyskal 1972*c*

30. Frontal vitta bare (Fig. 7). All bristles of head and body yellowish to brown 31

Frontal vitta with fine setae. Usually some black bristles present on head and body 32

31. Facial carina strongly broadened on lower half (Fig. 7). Wing with overall pattern ...... ***Gymnocarena*** Hering

3 spp.; central North America; Foote 1960*g*

Facial carina not strongly broadened on lower half. Wing proximal to crossvein dm-cu, except pterostigmal area, hyaline ...... ***Mylogymnocarena*** Foote

2 spp.; Arizona, Colorado; Foote 1960*g*

32. Posterior pair of scutellar bristles absent or distinctly shorter than anterior scutellar bristles. Two to four pairs of frontal bristles present. First flagellomere shorter than half height of eye ...... ***Eurosta*** Loew

9 spp.; widespread; Steyskal and Foote 1977

Posterior pair of scutellar bristles about as long as anterior scutellar bristles. Frontal bristles and first flagellomere variable 33

33. First flagellomere about three-quarters as long as height of eye, and acute at dorsal apex. Three or four pairs of frontal bristles present ...... ***Acidogona*** Loew

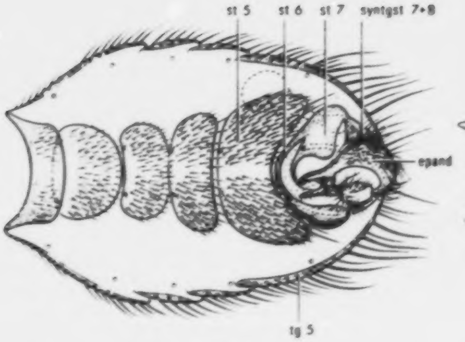
1 sp., *melanura* (Loew); Massachusetts to Florida; Benjamin 1934

First flagellomere less than half as long as height of eye. Two to four pairs of frontal bristles present 34

34. Body and bristles wholly yellowish. Wing (Fig. 22) yellowish on disc, varied with irregular brown markings, and with border of apical half distinctly darkened; tip of cell r_{4+5} with transverse brown band (Fig. 22) ...... ***Icterica*** Loew

2 spp.; eastern and central; Steyskal and Foote 1962, B. A. Foote 1967

Not as above 35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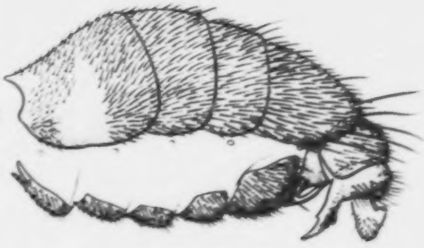
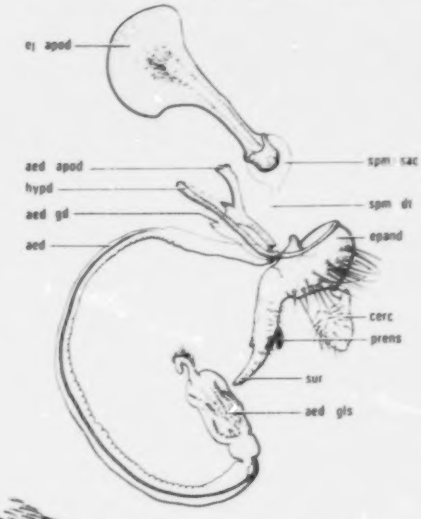
38 Rhagoletis pomonella ♂



39 Rhagoletis pomonella ♂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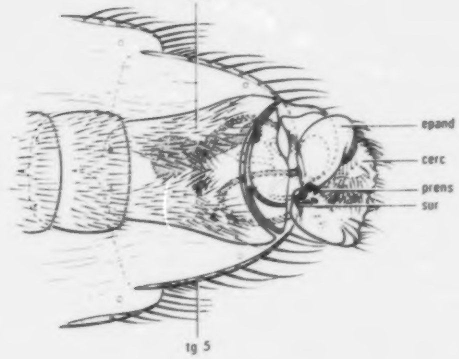
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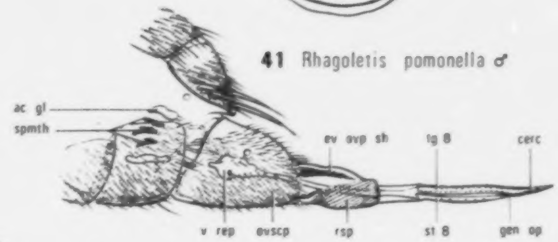
40 Euaresta aequalis ♂

41 Rhagoletis pomonella ♂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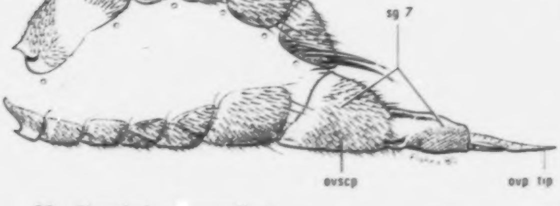
43 Rhagoletis pomonella ♀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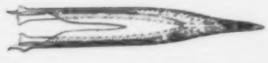

42 Rhagoletis pomonella ♀

44 Rhagoletis pomonella ♀

Figs. 66.38–44. Abdomens and terminalia: (38) ventral and (39) left lateral views of male abdomen of *Rhagoletis pomonella* (Walsh); (40) male terminalia of *Euaresta aequalis* (Loew), ventral view; (41) details of male terminalia of *Rhagoletis pomonella*, left lateral view; (42) female abdomen and (43) female terminalia of *R. pomonella*, left lateral view; (44) tip of ovipositor of *R. pomonella*, dorsal view.

Abbreviations: ac gl, accessory gland; aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; aed gls, aedeagal glans; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; ev ovp sh, eversible ovipositor sheath; gen op, genital opening; hypd, hypandrium; ovp, ovipositor; ovscp, oviscape; prens, prensiseta; rsp, rasper; sg , segment; spm dt, sperm duct; spm sac, sperm sac; spmth, spermatheca; st, sternite; syntgst, syntergosternite; sur, surstylus; tg, tergite; v rep, ventral receptacle.

35. Two pairs of frontal bristles present, both black; inner vertical bristle black; lower orbital bristle black; upper orbital bristle whitish. Apex of cell r_{4+5} with small round hyaline spot (Fig. 23) .... ***Xanthomyia*** Phillips

2 spp.; west to Idaho, south to Virginia; Foote 1964

Three or four pairs of frontal bristles present, blackish or whitish. Otherwise not as above 36

36. All frontal and orbital bristles usually whitish to light brown, not blackish. Apex of cell r_{4+5} usually with very narrow transverse hyaline band (Fig. 24) .... ***Jamesomyia*** Quisenberry

1 sp., *geminata* (Loew); eastern; Quisenberry 1949*a*

All frontal and orbital bristles blackish. Apex of cell r_{4+5} dark brown, with or without round hyaline spot .... ***Xenochaeta*** Snow

2 spp.; far western North America; Foote 1960*g*, Foote and Blanc 1979

37. Width of frons at vertex much less than width of eye in same plane. Acrostichal bristles in line with or anterior to wing base .... ***Xanthaciura*** Hendel

4 spp.; 3 spp. in southeast and 1 sp. extending westward to Missouri and Utah; Aczél 1949 and 1952*b*, Benjamin 1934

Not as above 38

38. Only one pair of scutellar bristles present 39

Two pairs of scutellar bristles present; posterior pair sometimes quite small 42

39. Cell r_{4+5} without bulla; dark coloring of wing forming stellate pattern in apical half of disc; tip of cell r_{4+5} usually hyaline, with proximal half usually unmarked, except often in cell sc and on lower margin of cell dm (Fig. 25) .... ***Trupanea*** Schrank

21 spp.; widespread; Malloch 1942, Foote 1960*f*

Cell r_{4+5} usually with bulla (Fig. 28); if bulla indistinct, tip of cell r_{4+5} dark brown; apex of wing with or without stellate pattern (Figs. 26, 27) 40

40. Abdomen pruinose. Extreme base of wing hyaline; apex with stellate pattern; tip of cell r_{4+5} hyaline .... ***Dyseuaresta*** Hendel

1 sp., *mexicana* (Wiedemann); Florida to Arizona; Benjamin 1934

Abdomen polished, at least in large part. Cell dm dark, with single round preapical hyaline spot; tip of cell r_{4+5} hyaline (Fig. 26) or not (Fig. 27) 41

41. Tip of cell r_{4+5} hyaline between arms of V-shaped dark mark (Fig. 26) .... ***Valentibulla*** Foote & Blanc

6 spp.; western; Foote and Blanc 1959 and 1979, Steyskal and Foote 1977

Tip of cell r_{4+5} dark brown to hyaline without V-shaped mark (Fig. 27) .... ***Aciurina*** Curran

about 12 spp.; western U.S.A.

42. Each side of frons with one well-developed black orbital bristle and one well-developed black frontal bristle, exclusive of weaker whitish orbital and frontal setulae. Labella elongate .... ***Oxyna*** Robineau-Desvoidy

3 spp.; western; Quisenberry 1949*c*

Bristles of frons and other characters not as above 43

43. Three pairs of whitish, relatively similar orbital bristles present; three pairs of frontal bristles present, the upper two strong and black, the lower one weak and whitish. Face with central black spot. Wing as in Fig. 28 .... ***Paracantha*** Coquillett

5 spp.; widespread except in northeast; Malloch 1941, Aczél 1952*a*

Two pairs of orbital bristles present; lower one, at least, blackish. Otherwise differing from above 44

44. Wing with four strongly oblique yellow and brown bands (Fig. 29) .... ***Tomoplagia*** Coquillett

2 spp.; north to Nevada, New York; Aczél 1955*a*, 1955*b*

Wing not banded 45

45. Two pairs of inclinate frontal bristles present 46

Three pairs of inclinate frontal bristles present 52

46. Lower facial margin weakly projecting. Wing with reticulate pattern (Fig. 30). Male fore femur swollen. Male terminalia broadened, with conspicuous striations in anal region (Fig. 40) .... ***Euaresta*** Loew
8 spp.; widespread; Quisenberry 1950

Not as above 47

47. Proboscis never geniculate. Cell sc usually mostly dark, never with a central round hyaline spot (Fig. 32). Hind femur usually with one preapical dorsal seta .... ***Tephritis*** Latreille
18 spp.; widespread; Quisenberry 1951, Foote 1960*d*, Foote and Blanc 1979

Proboscis geniculate; labella usually elongate (Fig. 3). Hind femur with more than one preapical dorsal seta, with the distal two side by side, or none at all present 48

48. C bowed anteriorly between subcostal break and apex of R_{2+3}, causing cell r_1 to be distinctly wider than cell r_{2+3} at level of apex of cell sc .... ***Gonioxyna*** Hendel
1 sp., *fuscata* Foote; California, Oregon, Wyoming; Foote and Blanc 1979

C not distinctly bowed anteriorly between subcostal break and apex of R_{2+3}; cell r_1 and cell r_{2+3} about equal in width at level of cell sc 49

49. Head distinctly longer than high (Fig. 3). Cell sc dark centrally, hyaline at extreme base and apex. Stem of aedeagus without setae .... ***Dioxyna*** Frey
2 spp.; 1 sp. widespread and the other known in Florida; Novak 1974

Head rarely longer than high, never markedly so. Cell sc usually with central round hyaline spot (Fig. 33). Stem of aedeagus with setae near tip before glans .... ***Paroxyna*** Hendel
22 spp.; mostly western; Novak 1974, Foote and Blanc 1979

50. Apex of cell r_{4+5} dark 51

Apex of cell r_{4+5} with at least a small hyaline spot, often more broadly hyaline 52

51. Hyaline spots in anterior half of wing disc bordered with darker brown than the yellowish brown background of disc; some small yellowish brown spots also present in disc .... ***Acinia*** Robineau-Desvoidy
1 sp., *picturata* (Snow); New York to Florida to southern California; Benjamin 1934, Aczél 1958

Hyaline spots in wing disc not bordered with darker brown; all spots hyaline or nearly so (Fig. 34) .... ***Neotephritis*** Hendel
3 spp.; mainly western; Foote 1960*e*, Steyskal 1972*b*

52. Wing disc almost completely bordered with brown, leaving large uninterrupted hyaline area occupying cells br, r_{4+5}, and dm .... ***Metatephritis*** Foote
1 sp., *fenestrata* Foote; California, Wyoming; Foote 1960*g*

Wing pattern otherwise 53

53. Hyaline spot in apex of cell r_{4+5} usually as long as wide, bordered by relatively narrow dark arms terminating at apices of R_{4+5} and M (Fig. 35) 54

Hyaline spot in apex of cell r_{4+5} either part of more extensive hyaline area or represented only by a small spot 55

54. R_{4+5} strongly setose over most of length; dark brown color of wing disc extensive, contrasting markedly with the relatively small well-defined hyaline markings .... ***Tetreuaresta*** Hendel
more than 17 neotropical spp., 4 spp. in Mexico; Steyskal 1972*a*

R_{4+5} with at most only a few small setae near base; contrast in wing colors not as marked as above .... ***Euarestoides*** Benjamin
4 spp.; widespread; Foote 1958, 1962

55. Wing disc with several large dark markings anteriorly and three light brown transverse bands in apical third (Fig. 37) .... ***Acrotaenia*** Loew
1 sp., *testudinea* (Loew); Florida; Foote 1960*g*

Wing pattern otherwise; an extensive hyaline area present at wing apex 56

56. Wing dark to extreme base; disc usually with many very small hyaline to yellowish spots; uniformly hyaline arc present at wing apex (Fig. 36) .... ***Eutreta*** Loew
17 spp.; widespread; Stoltzfus 1977, Foote and Blanc 1979

Wing hyaline in basal one-fourth or one-fifth; hyaline area at wing apex usually containing dark spots at apices of R_{4+5} and M .... ***Cryptotreta*** Blanc & Foote
2 spp.; California; Steyskal and Foote 1977

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RICHARDIIDAE

67

George C. Steyskal

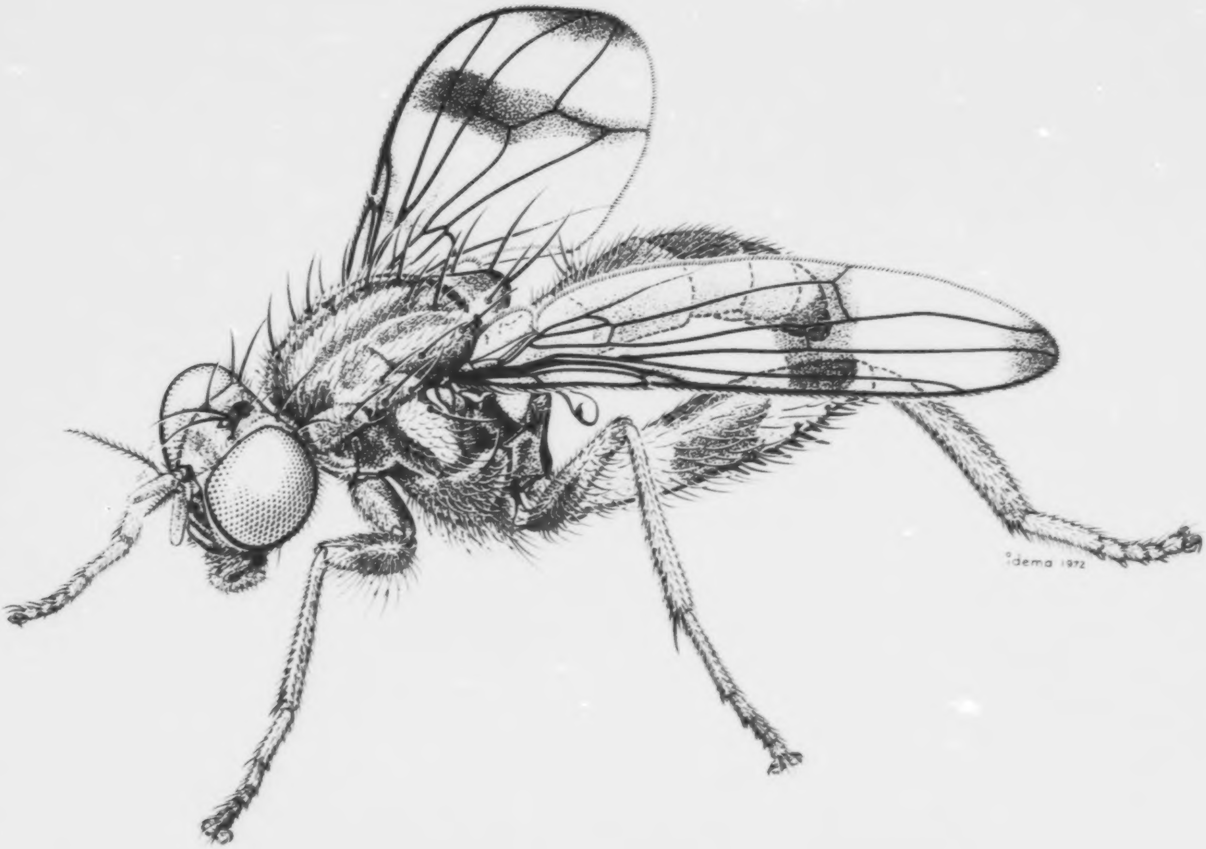


Fig. 67.1. Adult male of *Richardia eburneosignata* Hennig.

Flies ranging from 3.25 to about 15 mm in body length, usually rather slender, especially in larger species (Fig. 1). Color ranging from yellowish through various combinations of that color, brown, and black to wholly black, with some parts such as femora and abdomen bright metallic blue. Wings usually with brown spots or bands. Some species strongly sexually dimorphic. Male of *Omomyia* Coquillett, especially *O. hirsuta* Coquillett, differing considerably from female in general appearance, having all hairs lengthened and apically sinuous, and with scutellum elongated (Figs. 8, 9).

Adult. Head: roundish (Figs. 9–13), but sometimes, as in *Coniceps* Loew (Fig. 13), swollen behind eyes and extended before eyes into a dorsoventrally flattened wedge. Male of some Neotropical species of *Richardia* Robineau-Desvoidy with stalked eyes, and in one species, male with long genal processes. Antenna of moderate length, never very short, and sometimes a little elongate; first flagellomere usually longest, with subbasal dorsal arista. Proboscis short; palpus well-developed. Chaetotaxy: usually one pair each of inner and outer vertical bristles, one pair of large ocellar bristles, zero or one pair of small postocellar bristles, and one pair of reclinate orbital bristles present; frontal bristles and vibrissae absent.

Thorax: somewhat depressed and usually a little longer than broad, or elongate and tapering forward. Pleuron high. Scutellum short and convex, except in male of *Omomyia hirsuta*, where it is elongate, laterally concave, and squarely truncate at apex between apical pair of bristles (Fig. 8). Subscutellum weakly to strongly developed. Rear of thorax between hind coxae and abdomen sclerotized from side to side, except in Epiplateinae, *Melanoloma* Loew, and perhaps in some specimens of *Setellida caerulescens* Hendel. Chaetotaxy: disc of proepisternum bare or setulose; one proepisternal, one katepisternal, and one anepisternal bristle sometimes present; anepimeron bare; one or two postpronotal and one or two notopleural bristles present; one presutural supra-alar bristle sometimes present; one or two postsutural dorsocentral, one postsutural supra-alar, and one postalar bristle present; postsutural intra-alar bristle present or absent; one or two scutellar bristles present; bristles in male of *Omomyia hirsuta* sometimes difficult to distinguish from abundant long hairs. Posterior thoracic spiracle frequently with at least one fine bristle arising on posteroventral margin.

Legs usually of ordinary length or somewhat elongate. Hind femur distinctly thickened in *Richardia* species; all or no femora usually with one to several stout ventral setae.

Wing (Figs. 2–7) of ordinary shape or somewhat elongate, sometimes tapering to base, and with alula greatly reduced. C always with subcostal break, sometimes also with humeral break; costal margin with row of distinctly stronger and more erect setae only in *Omomyia* species (Fig. 3) and indistinctly in male of some specimens of Neotropical species, e.g. *Epiplatea erosa* Loew; Sc complete to C in Epiplateinae (Figs. 2, 3), but also interrupted next to subcostal break in Richardiinae (Figs. 4–7). Pterostigmal area short and narrow. R_1 a little sinuate opposite subcostal break, bare or setose. Cell cu*p* more or less rounded apically, closed by somewhat retrorse vein.

Abdomen: oval to petiolate or parallel-sided, often with one or a few conspicuous preapical lateral bristles on tergite 2. Male terminalia (Figs. 14, 15) in repose twisted down and forward; seven spiracles present; aedeagus long and coiled, with simple or distinctly specialized tip. Female terminalia (Figs. 16, 17) with ovipositor ending in piercer formed from fused cerci in Richardiinae and with separate, although sometimes closely adjacent, cerci in Epiplateinae (Fig. 17). Oviscape fused laterally in all species examined; suture shown by Steyskal (1973) for *Omomyia hirsuta* as open for most of its length is in reality a pale strip of well-sclerotized cuticle (Fig. 16); in *O. regularis* Curran, this line of fusion barely evident. Two globular spermathecae present.

Egg. Those known taken from abdomen of a specimen of *Automola rufa* Cresson. These about 0.68 mm long, paraboloid at each end, with no evident chorionic sculpturing.

Puparium. That of *Epiplatea hondurana* Steyskal described and illustrated by Steyskal (1958) as generally acalyptrate in form, about 4 mm long, circular in cross section, with few distinctive characters. Posterior spiracles consisting of two sets of three nearly horizontal slits that slightly increase in length from dorsal one to ventral one; anterior spiracles having 10–12 papillae arranged in about two-thirds of a circle.

Biology and behavior. Very little is known of the biology of any of the Richardiidae. The only immature forms known are puparia of *Epiplatea hondurana*, taken from a diseased *Cocos nucifera* (coconut palm) (Steyskal 1958). Species of *Omomyia* seem to have some kind of association with *Yucca* (McAlpine 1976), and several species of the family have been taken at flowers. Unpublished data indicate that larvae of a species of *Odontomera* Macquart destroy the growing tips of a grass, and larvae of some species of *Beebeomyia* Curran live in the flowers of Araceae, Marantaceae, and Musaceae.

Classification and distribution. The Richardiidae comprise 170 species and are restricted to the Americas. Only ten species in six genera have been found as far northward as the United States and southernmost Canada. The taxonomy of the family is based on two works by Hendel (1911*a*, 1911*b*), one by Enderlein (1912), and a series of four by Hennig (1937–1938). The species were cataloged by Aczél (1950) and Steyskal (1968). The family was at first considered a subfamily of the Otitidae, but it is now generally accorded familial rank. J. F. McAlpine (1976) convincingly showed that *Omomyia* should be transferred from the Thyreophoridae to the Richardiidae and suggested that the genera *Automola*, *Epiplatea*, and *Omomyia* may be worthy of distinction as a subfamily. That suggestion is adopted here by placing those genera in the new subfamily Epiplateinae as a plesiomorphic sister group to the remainder of the family.

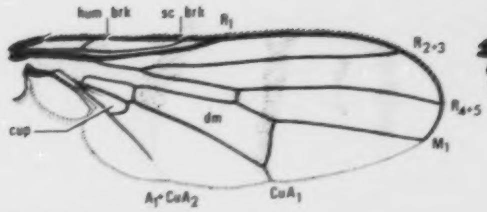
Key to genera

1. Femora without stout ventral setae. Sc complete to C just distal of subcostal break (Figs. 2, 3). Thorax between hind coxae and abdomen broadly membranous medially. Male with aedeagus simple at tip, at most only slightly specialized; female ovipositor with separate cerci (Fig. 17) .... EPIPLATEINAE....2

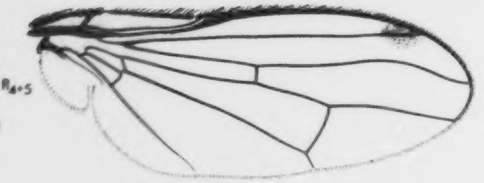
Femora with stout ventral setae on at least one pair (except in most species of *Setellia* Robineau-Desvoidy). Sc interrupted adjacent to subcostal break (Figs. 4–7). Thorax sclerotized medially between hind coxae and abdomen (except, so far as is known, in *Melanoloma* and perhaps in some specimens of *Setellida caerulescens*). Male with aedeagus distinctly specialized at tip (Fig. 14); female with cerci fused to form piercing ovipositor .... RICHARDIINAE ...3

2. R_1 setose; C finely and uniformly clothed with reclinate setulae; wing with conspicuous pattern including complete dark brown crossbands (Fig. 2) .... ***Automola*** Loew

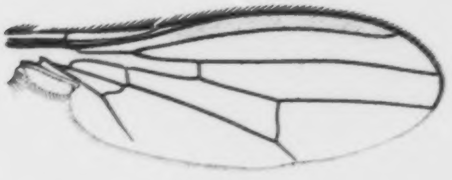
1 sp., *rufa* Cresson; New Mexico, Texas (other species south of U.S.A.); Steyskal 1958



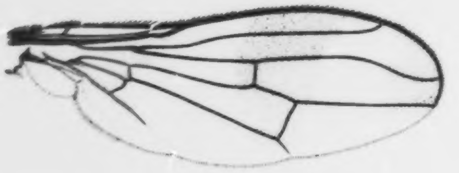
2 Automola rufa ♀



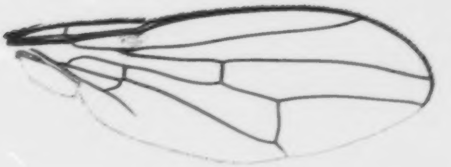
3 Omomyia hirsuta ♀



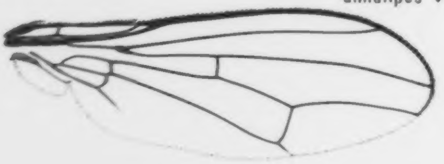
4 Coniceps niger ♀



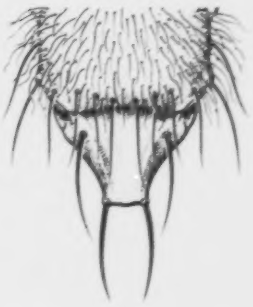
5 Richardia teevani annulipes ♀



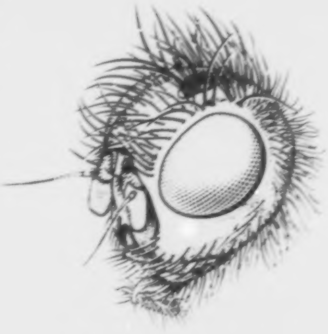
6 Odontomera ferruginea ♀



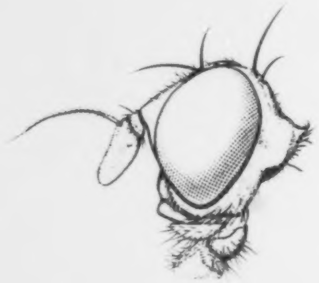
7 Sepsisoma flavescens ♀



8 Omomyia hirsuta ♂



9 Omomyia hirsuta ♂



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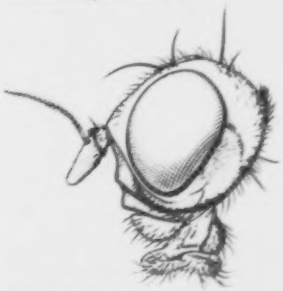
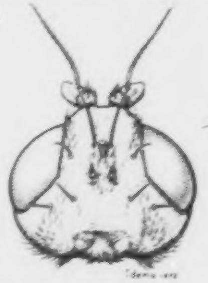
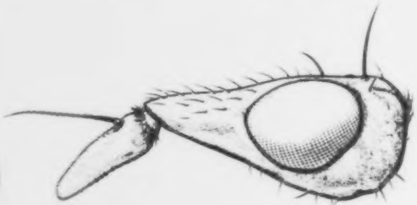


11 Sepsisoma flavescens ♂



12 Sepsisoma flavescens ♂



13 Coniceps niger ♂

Figs. 67.2–13. Wings, scutellum, and heads: wings of (2) *Automola rufa* Cresson, (3) *Omomyia hirsuta* Coquillett, (4) *Coniceps niger* Loew, (5) *Richardia teevani annulipes* Curran (Neotropical), (6) *Odontomera ferruginea* Macquart, and (7) *Sepsisoma flavescens* Johnson; (8) scutellum of *Omomyia hirsuta*, dorsal view; heads of (9) *Omomyia hirsuta* in left anterolateral view, (10) *Odontomera ferruginea* in left lateral view, (11) *Sepsisoma flavescens* in left lateral view, (12) *Sepsisoma flavescens* in dorsal view, and (13) *Coniceps niger* in left lateral view.

Abbreviations: hum brk, humeral break; sc brk, subcostal break.

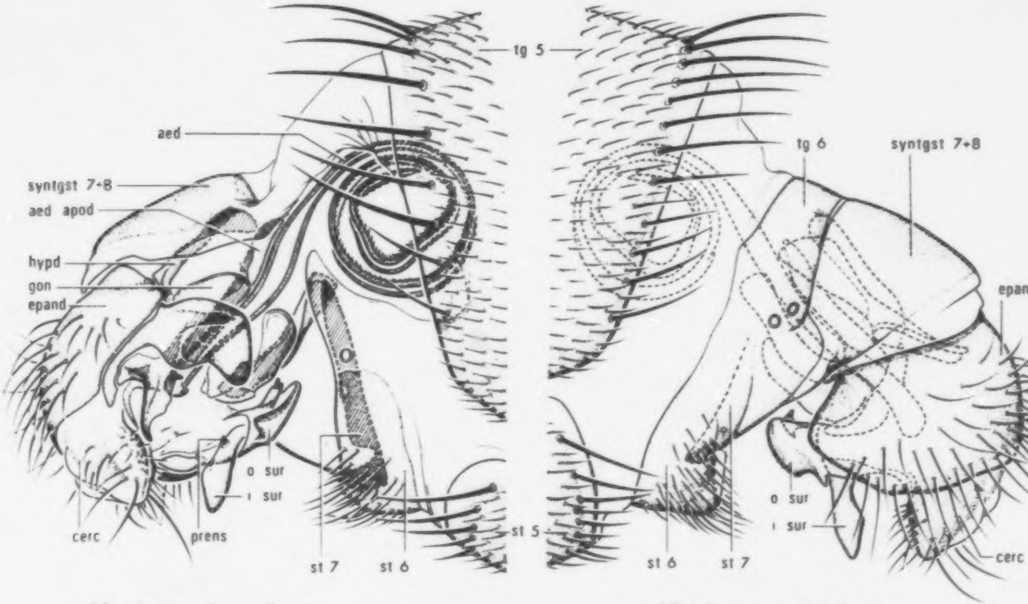
R_1 not setose; C with fine reclinate setulae and at least several more widely spaced, more erect, stronger setae; wing pattern consisting only of infuscate costal cells and a brown spot at tip of R_{2+3} (Fig. 3) .... ***Omomyia*** Coquillett

3 spp.; California to New Mexico; Steyskal 1973

3. Head twice as long as high; frons projecting well beyond eyes (Fig. 13). Ocellar triangle and orbital bristle posterior to middle of eyes. Vein A_1 complete to wing margin (Fig. 4) .. .. ***Coniceps*** Loew

1 sp., *niger* Loew; from South Dakota to Texas; Steyskal 1958

Head not much longer than high; frons no more than slightly projecting (Figs. 10, 11). Otherwise various 4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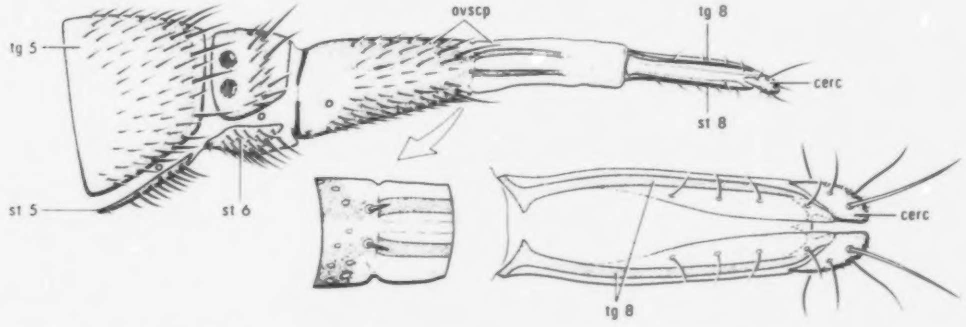
14 Automola rufa ♂

15 Automola rufa ♂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16 Automola rufa ♀

17 Automola rufa ♀

Figs. 67.14–17. Terminalia: (14) right lateral and (15) left lateral views of male terminalia of *Automola rufa* Cresson; (16) left lateral and (17) dorsal views of female terminalia of *A. rufa*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; i sur, inner surstylus; o sur, outer surstylus; ovscp, oviscape; prens, prensiseta; st, sternite; syntgst, syntergosternite; tg, tergite.

4. Hind femur considerably thicker than others ....***Richardia*** Robineau-Desvoidy
mainly Neotropical, with 1 sp., *eburneosignata* Hennig, as far north as Texas; Steyskal 1977
All femora of similar thickness 5

5. Occiput more swollen below than above neck (Fig. 10) ....***Odontomera*** Macquart
2 spp.; New Jersey to Florida (others Neotropical); Steyskal 1958
Occiput more swollen above than below neck (Figs. 11, 12) ....***Sepsisoma*** Johnson
3 spp.; southern Ontario, New York to Iowa and southward (others Neotropical); Steyskal 1961

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PALLOPTERIDAE

68

J. F. McALPINE

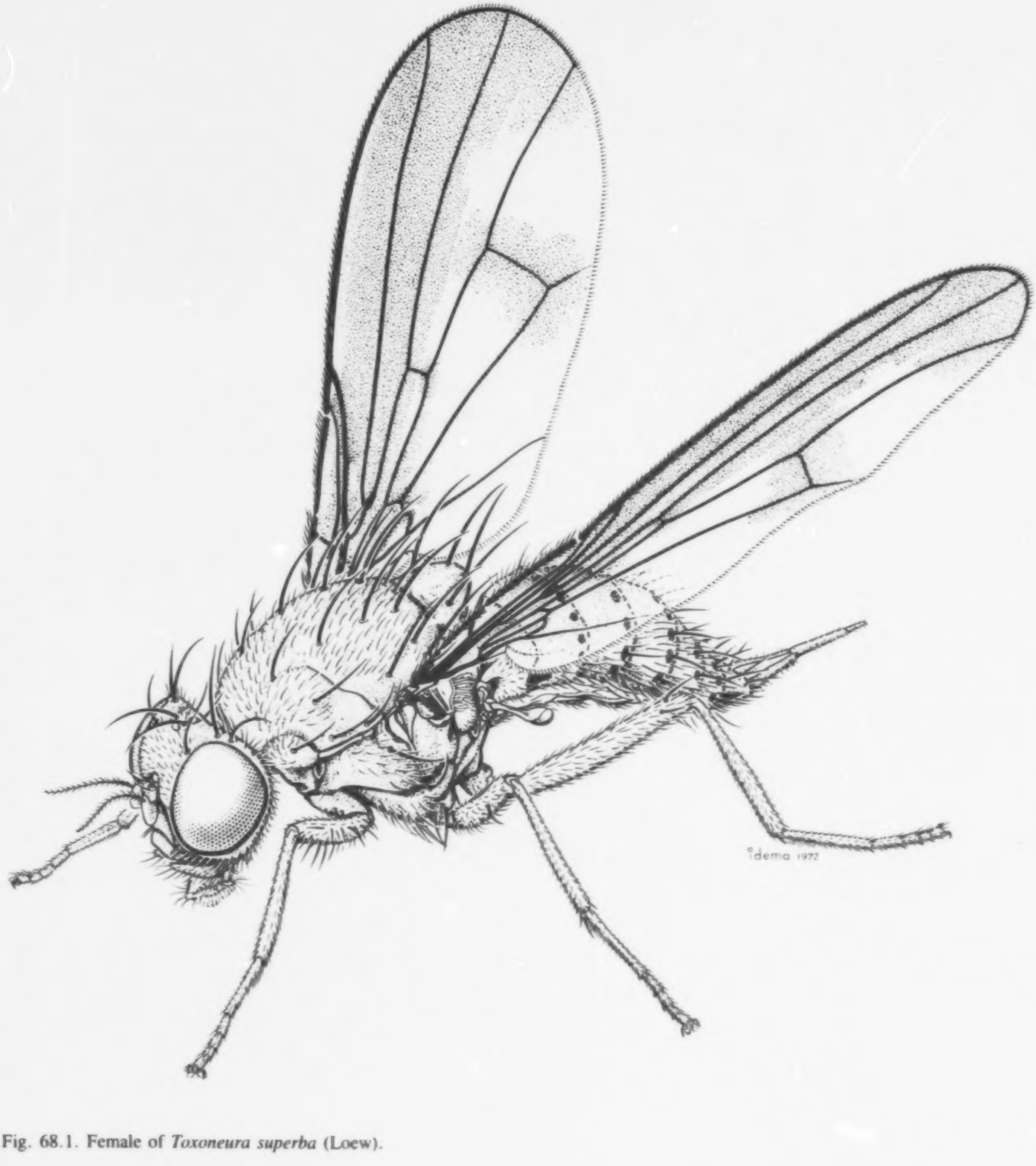


Fig. 68.1. Female of *Toxoneura superba* (Loew).

Medium-sized otitid-like flies (Fig. 1), 3-5 mm long, grayish or yellowish, usually with brownish-marked wings and simple legs.

Adult. Head: scarcely as broad as thorax, usually higher than long (Fig. 1). Frons broader than high, usually of same width in both sexes, always yellowish at least on anterior half; interfrontal area finely setulose or bare; orbital plate usually weakly differentiated, reaching only slightly below level of anterior ocellus; a single reclinate or lateroreclinate orbital bristle present; ocellar and inner and outer vertical bristles strong; postocellar bristles present but weaker, slightly divergent; lunule linear, unexposed, without setulae. Face somewhat sunken, gently convex, always yellowish, usually with a weak median carina, without hairs or bristles; parafacial linear to moderately broad, without hairs or bristles. Clypeus moderately large; oral vibrissae absent; cheek almost linear to about half height of eye in width; series of fine subvibrissal setulae present, among which are two outstanding distantly separated genal bristles. Compound eye usually nearly round, bare, unpatterned. Antenna short; scape very short, with few fine setulae; pedicel notched on apicodorsal margin, with one bristle and a row of fine setulae along apical margins; first flagellomere usually slightly longer than broad; arista almost bare to shortly plumose. Proboscis short, with well-developed labella; palpus usually moderately large, rarely strongly enlarged.

Thorax: blackish to yellowish in background color, usually pruinose, sometimes polished, occasionally patterned in black and yellow, with yellowish or blackish setulae or bristles or some combination of them. Scutum moderately strongly arched (Fig. 1); scutellum usually with convex disc; prescutellum undeveloped; subscutellum moderately well-developed. Prosternum rather narrow, free from proepisternum. Chaetotaxy: one postpronotal and one presutural intra-alar bristle, one presutural and three postsutural dorsocentral bristles, one or two prescutellar acrostichal and two supra-alar bristles, one postsutural intra-alar bristle, one lateral and one subapical scutellar bristle, and two notopleural bristles present; one strong to weak proepisternal bristle present; one weak proepimeral bristle present or absent; anepisternum setulose or bare, with or without one or more strong bristles posteriorly; katepisternum with one bristle and numerous setulae; anepimeron bare; prosternum usually with a few fine setulae; metasternal area bare.

Wing (Fig. 1) moderately long, usually rather narrow but with well-developed anal angle and alula, and variously patterned with brown spots to almost entirely hyaline; cell sc always darkened. C without spines in Nearctic genera, with costagial, humeral, and subcostal weakenings or breaks, and ending rather abruptly just beyond insertion of R_{4+5}; Sc complete; base of R bare, with R_1 ending well beyond insertion of Sc but far before middle of wing; cells bm and dm present and separated by crossvein bm-cu; crossvein r-m joining cell dm at or near midpoint; crossvein dm-cu nearly parallel to crossvein r-m, always closer than its own length to wing margin; cell cup convexly closed; A_1 reaching or nearly reaching wing margin at least as a fold. Alula large. Upper calypter moderately large, with fringe of longish silky hairs; lower calypter linear. Halter entirely whitish.

Legs fairly slender. Fore femur with a row of posterodorsal and posteroventral bristles; mid femur usually with one preapical dorsal, one or two anterodorsal, and one anteroventral bristle. Tibiae usually yellowish, without preapical dorsal bristles (except in Palaearctic *Eurygnathomyia bicolor* (Zetterstedt)); mid tibia with a fairly strong apicoventral bristle. Tarsi slender, frequently mainly yellowish.

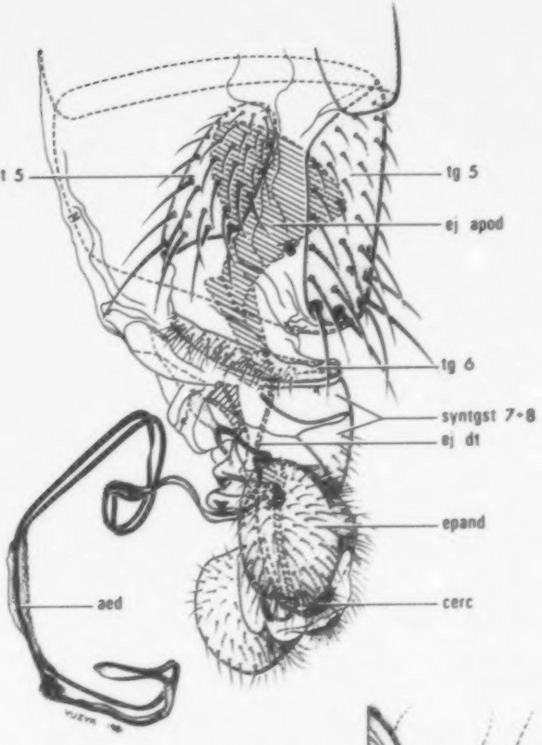
Abdomen: subcylindrical, dark brown to yellow, seldom patterned.

Male (Figs. 2, 3) usually with five pairs of spiracles in membrane (six pairs in *Eurygnathomyia* Czerny). Tergite 6 usually absent; sternite 6 asymmetric, shifted into left side of abdomen. Syntergosternite 7 + 8 large, setulose dorsally. Epandrium large, with rather globose sides. Surstylus absent or indistinguishably fused with lateral margins of epandrium in Nearctic genera, well-developed in some extralimital genera. Hypandrium small, with large median hypandrial apodeme; gonopod small, finely setulose, weakly sclerotized and lobe-like (Fig. 4) in Nearctic genera, divided and complex in some extralimital genera; paramere (Fig. 4) usually extremely reduced and finely setulose, absent in *Eurygnathomyia*, but strongly developed in southern genera; aedeagus long, convoluted in Nearctic genera, finely to coarsely setulose or almost bare, frequently with an enlarged complicated apical glans; epiphallus absent in Nearctic genera, but present in Palaearctic and Neotropical genera; aedeagal apodeme rod-like; ejaculatory apodeme heavily sclerotized, usually rather large. Sternite 10 (Fig. 4) well-developed in Nearctic genera, sometimes with paired stout spines at anterior margin. Cerci small and lobe-like in Nearctic genera, large and elongate in some extralimital genera.

Female (Fig. 6) with sternite 7 and tergite 7 fused laterally to form stout oviscape and enclosing seventh pair of abdominal spiracles. Ovipositor shaft-like, with cerci fused to form apical point (Fig. 5). Two sclerotized spermathecae present in Nearctic genera and three in *Morgea* Hennig and *Sciochthis* Malloch.

Larva. Typical of several acalyptrate families including Chloropidae and Lonchaeidae (Morge 1956, Teskey 1976). Cephalopharyngeal skeleton consisting of paired simple mandibles and dental sclerites, parastomal bars, and a hypopharyngeal sclerite that is clearly separated from pale tentoropharyngeal sclerite. Anterior spiracles fan-shaped, each with five or six papillae. Creeping spines present only anteroventrally on seven or eight abdominal segments. Terminal abdominal segment bluntly rounded posteriorly, without tubercles, but with stump-like projections bearing spiracles.

Biology and behavior. The biology of the family was summarized by Teskey (1976). Morge (1956, 1967*a*) reported larvae of two species of *Palloptera* Fallén living under bark of dead coniferous and deciduous trees in Europe,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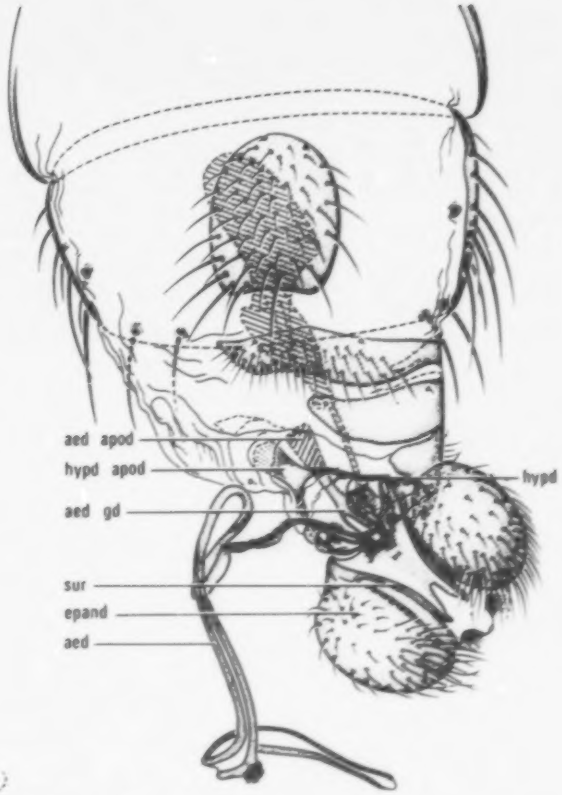
2 Toxoneura superba ♂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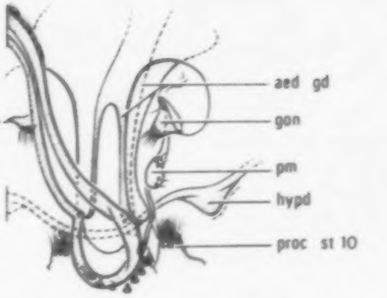
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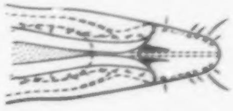
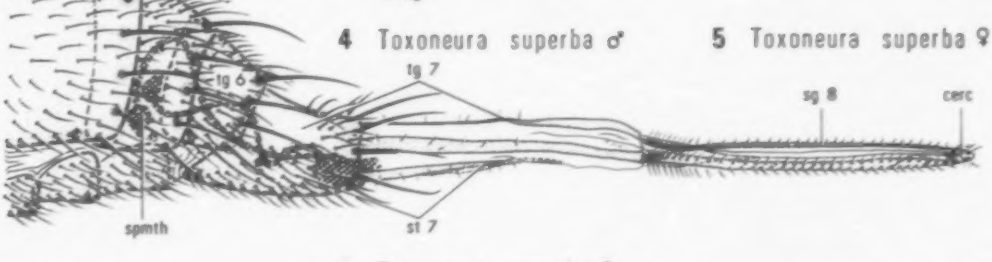
4 Toxoneura superba ♂



5 Toxoneura superba ♀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6 Toxoneura superba ♀

Figs. 68.2–6. Male and female terminalia of *Toxoneura superba* (Loew): (2) left lateral view of male; (3) ventral view of male; (4) enlargements of parts at base of aedeagus; (5) dorsal view of apical segment of ovipositor; (6) left lateral view of ovipositor and associated parts.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; hypd apod, hypandrial apodeme; pm, paramere; proc, process; sg, segment; spm dt, sperm duct; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

preying on the larvae of Cerambycidae and Scolytidae. Mark Deyrup of Washington State University (personal communication) confirmed that at least some North American species have similar habits when he reared an adult of *Palloptera* from a larva found in galleries of the scolytid *Pityophthorus pseudotsugae* in *Abies procera* (noble fir). Keen (1958) reared an undetermined species of *Palloptera* from cones of *Abies concolor* (white fir) and A. F. Hedlin (unpublished) reared many adults of *P. claripennis* Malloch from larval stages that preyed on larvae of *Contarinia oregonensis* Foote, in cones of *Pseudotsuga menziesii* (Douglas fir) near Victoria, British Columbia. Several European species have been reared from larvae found in flower heads and stems of Compositae and Umbelliferae, and it is suspected that *P. scutellata* Macquart is associated with *Juncus* species (Stubbs 1969). Adults are usually taken while resting on low branches and flowers. *Toxoneura superba* (Loew) is sometimes attracted to lights.

Classification and distribution. The family Pallopteridae, sometimes called the flutter fly family because of the way the males vibrate their wings, is most closely related to the Piophilidae and Richardiidae. Its sister family is the Piophilidae, and the two families together comprise the sister group of the Richardiidae (McAlpine 1976, 1977, 1981). The Pallopteridae contains the following genera: *Eurygnathomyia* and *Morgea* (Palaearctic); *Palloptera*, *Temnosira* Enderlein, and *Toxoneura* Macquart (Holarctic); *Aenigmatomyia* Malloch, *Heloparia* Enderlein, *Homaroides* Malloch, *Pseudopyrgota* Malloch, and *Sciochthis* Malloch (Neotropical); and *Neomaorina* Miller (New Zealand). In addition, three fossils from Baltic amber (Oligocene) are known (Hennig 1967): *Pallopterites electrica* Hennig, as well as *Morgea mcalpinei* Hennig, related to *Aenigmatomyia*, and *Glaesolonchaea electrica* Hennig; the latter two were originally placed in the Lonchaeidae and later transferred to the Pallopteridae (Morge 1967*b*). Two subfamilies are recognized (Morge 1967*b*); Eurygnathomyiinae, which was treated as a family by Griffiths (1972), containing only the genus *Eurygnathomyia*; and Pallopterinae, containing all the remaining genera. McAlpine (1981) provided a key to the world genera of the family. Representatives of only the genera *Palloptera*, *Temnosira*, and *Toxoneura* containing in all some 45 world species (17 Nearctic) have been found in the Nearctic region. The most recent treatment of the Nearctic species is by Malloch and McAtee (1924), but it is neither accurate nor complete; about eight undescribed species are now known and a revision of the American species is needed. Morge (1967*b*) gave a key to the Palaearctic species; Collin (1951) and Martinek (1977) provided useful treatments of the British and Czechoslovakian species, respectively.

Key to genera

1. Anepisternum bare .... ***Palloptera*** Fallén

4 spp.; widespread; Malloch and McAtee 1924

Anepisternum with bristles or setulae or both 2

2. Vestiture of anepisternum pale yellowish white. Scutum and scutellum mostly polished .... ***Temnosira*** Enderlein

1 sp., *subarcuata* Johnson; British Columbia to Nova Scotia, Maine, and New Hampshire

Vestiture of anepisternum blackish. Scutum and scutellum dull pruinose .... ***Toxoneura*** Macquart

4 spp.; widespread; Malloch and McAtee 1924

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PIOPHILIDAE

69

J. F. McALPINE

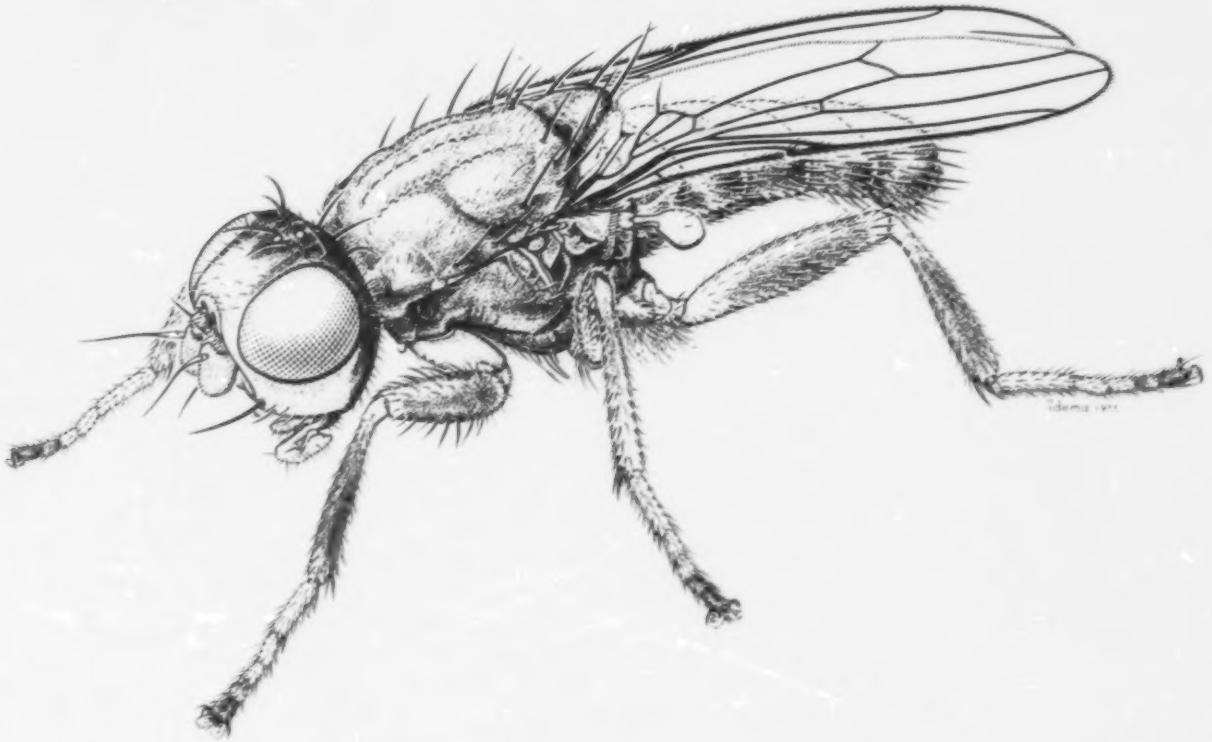
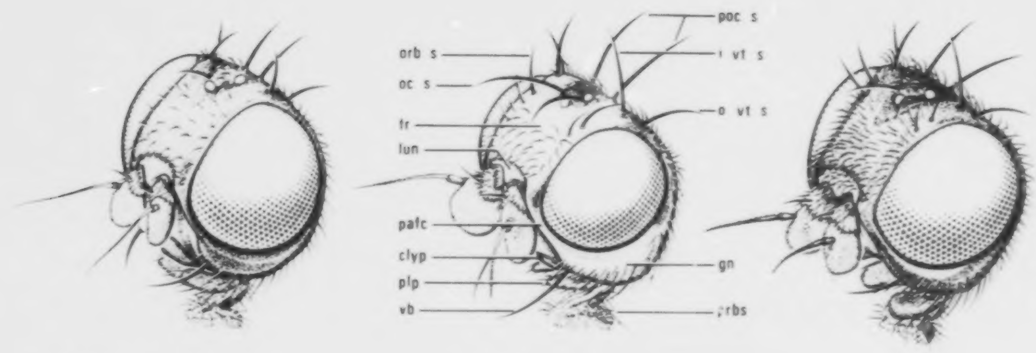


Fig. 69.1. Male of *Piophila casei* (Linnaeus).

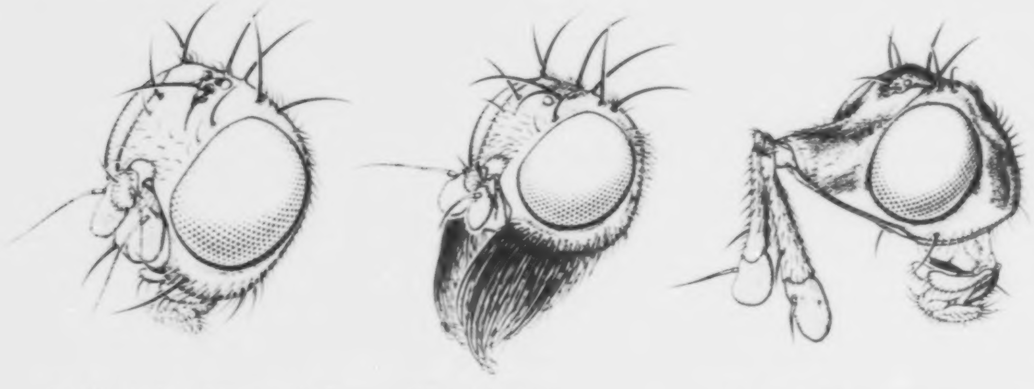
Moderately small flies, 3.0–6.0 mm long, shining black to dull brownish yellow, somewhat similar in general appearance (Fig. 1) to dung flies (Scathophagidae) and flutter flies (Pallopteridae). Body usually with fairly strong black bristles, sometimes densely hairy. Frons frequently conspicuously yellowish, at least on anterior half. Wing frequently glassy, sometimes with brown markings.

Adult. Head: scarcely as wide as thorax, usually higher than long in side view (Figs. 2–10). Compound eye nearly round, bare. Frons about as broad as long, similar in width in both sexes, wholly setulose; sides virtually parallel; anterior portion weakly sclerotized, usually yellowish; ocellar triangle and orbital plates heavily sclerotized and frequently contrasting in color with remainder of frons. Chaetotaxy: two or three orbital bristles present, usually outwardly directed; one pair of strong anterolaterally directed ocellar setae and several to many ocellar setulae present; inner and outer vertical bristles subequal; postocellar bristles divergent; vibrissae usually strong (Figs. 1–5), but weak in some *Prochyliza* Walker (Fig. 7), sometimes duplicated (Figs. 9, 10), and beard-like in males of *Amphipogon* Wahlberg (Fig. 6). Lunule usually bare, setulose in *Neopiophila* McAlpine (Fig. 4) and in some species of *Mycetaulus* Loew. Face concave, with rather deep antennal grooves. Clypeus rather small. Antenna short, porrect; first flagellomere usually oval, rarely twice as long as wide; arista bare or shortly pubescent, never plumose; pedicel usually about as long as wide, greatly elongated in male of *Prochyliza xanthostoma* Walker (Fig. 7), without a seam or lateral projections, usually with a conspicuous dorsal bristle; scape short, simple. Proboscis short, with membranous labella; palpus usually fairly small, enlarged in *Neopiophila setaluna* McAlpine (Fig. 4) and in the Australian species *Piophilosoma palpatum* (Hendel).

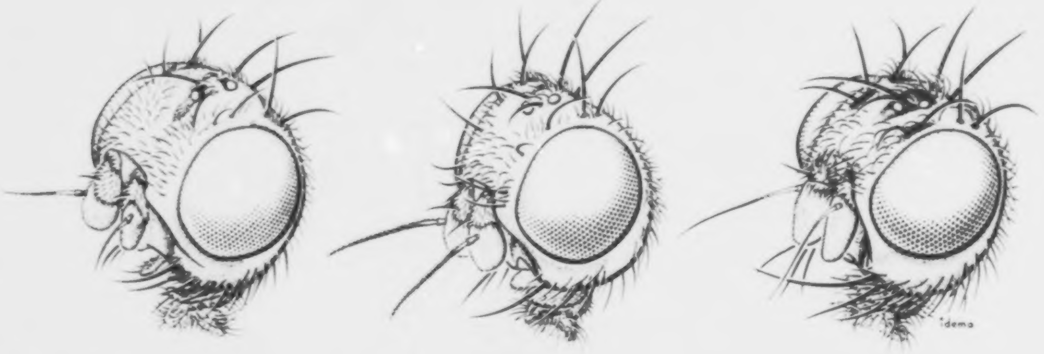
Thorax: scutum (Figs. 11, 12) densely hairy to almost bare, usually shining, heavily pruinose in a few species of *Mycetaulus* and in *Boreopiophila tomentosa* Frey; prescutellum absent; scutellum frequently flattened above (Fig. 14), lengthened in Thyreophorina, with a pair of tubercles in *Lasiopiophila* Duda (Fig. 13). Prosternum free from propleuron. Chaetotaxy: zero to two postpronotal, zero or one presutural intra-alar, usually one postsutural intra-alar, zero to three presutural dorsocentral, one to three postsutural dorsocentral, and two notopleural bristles present; postsutural acrostichal bristles present or absent; four



2 Stearibia nigriceps ♂ **3** Allopiophila luteata ♀ **4** Neopiophila setaluna ♀



5 Mycetaulus longipennis ♀ **6** Amphipogon hyperboreus ♀ **7** Prochyliza xanthostoma ♂



8 Neottiophilum praeustum ♂ **9** Actenoptera hilarella ♂ **10** Bocainamyia necrophila ♂

Figs. 69.2–10. Heads, left anterolateral view: (2) *Stearibia nigriceps* (Meigen); (3) *Allopiophila luteata* (Haliday); (4) *Neopiophila setaluna* McAlpine; (5) *Mycetaulus longipennis* Loew; (6) *Amphipogon hyperboreus* (Greene); (7) *Prochyliza xanthostoma* Walker; (8) *Neottiophilum praeustum* (Meigen) (Palaearctic); (9) *Actenoptera hilarella* (Zetterstedt); (10) *Bocainamyia necrophila* Albuquerque (Neotropical).

Abbreviations: clyp, clypeus; fr, frons; gn, gena; i vt s, inner vertical seta; lun, lunule; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; pafc, parafacial; plp, palpus; poc s, postocellar seta; prbs, proboscis; vb, vibrissa.

bristles on scutellum (Figs. 12–14), with (Fig. 13) or without additional hairs (Figs. 12, 14); anepisternum and anepimeron usually bare, sometimes setulose (Fig. 11); katepisternum with one to several bristles and numerous setulae; proepisternal bristle present; proepimeral bristle absent; prosternum usually bare, haired in *Neopiophila* and *Allopiophila* Hendel.

Wing (Figs. 15–19) moderately broad, with well-developed anal lobe and alula; membrane usually glassy hyaline, patterned in *Mycetaulus* (Fig. 17), *Neottiophilum* Frauenfeld (Fig. 19), and *Pseudoceps* Becker. C with subcostal break and attenuated but not broken at position of humeral break; costal spines present in *Neottiophilum* (Fig. 19) and *Piophilosoma* Hendel, extending as far as insertion of M. R_1 setulose in Neottiophilinae; all veins otherwise bare; Sc complete and free from R. Cells bm and dm separated by crossvein bm-cu; cell cu*p* complete. A_1 traceable to wing margin (Figs. 15–19) or abruptly discontinued before reaching wing margin (Fig. 1).

Legs rather stocky. Femora and tibiae simple; tibiae without preapical dorsal bristles but frequently with other rather strong bristles, especially ventrally and laterally near apex. Tarsi often strongly setulose, with unusually strong tarsal claws.

Abdomen: sparsely and shortly setulose to densely long-haired, shiny black to dull brownish yellow, unpatterned (Figs. 1, 22).

Male (Fig. 22) lacking sixth and seventh spiracles. Terminalia (Figs. 23–28) asymmetric; tergite 6 usually absent, but sometimes with fragments remaining at sides (Figs. 25, 28); left posterolateral margin of sternite 6 fused with sternite 7; sternite 7 likewise mostly fused with syntergosternite 8. Surstylus usually free and moveable, sometimes absent (*Actenoptera* Czerny), sometimes fused with epandrium (*Pseudoceps*). Cerci usually in form of simple membranous lobes. Hypandrium with gonopod and paramere usually well-developed, but sometimes reduced or absent (*Actenoptera*); aedeagus usually long and flexible (Fig. 27), frequently coiled, often pubescent, sometimes much reduced (*Neopiophila*, Figs. 23 and 24; *Actenoptera*), and with (Figs. 25–27) or without well-differentiated distal glans; aedeagal apodeme usually fused with hypandrium.

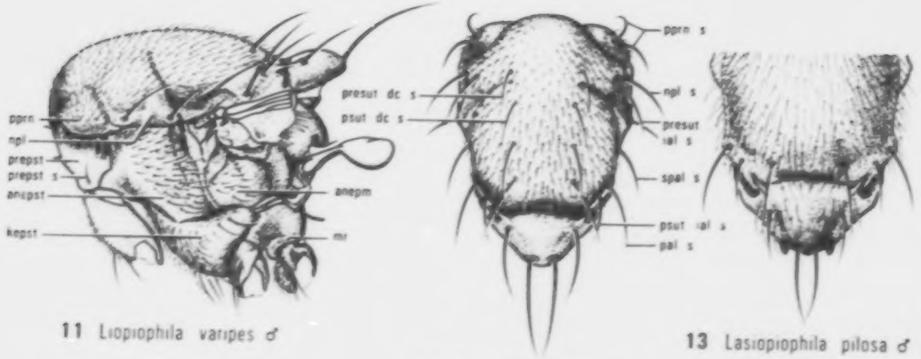
Female with a rather weakly sclerotized telescopic piercing ovipositor (Figs. 20, 21). Sixth and seventh spiracles present in membrane between corresponding tergites and sternites. Tergite 7 and sternite 7 free from each other, each with two strap-like rods arising from posterior margins to form flexible longitudinal struts. Tergite 8 and sternite 8 each in form of two similar elongate straps in membrane. Epiproct, hypoproct, and fused cerci forming tip of ovipositor. Two spermathecae present, usually elongate, sclerotized except in *Amphipogon*.

Larva. Maggot-like (Fig. 29), peg-shaped, tapering to anterior end, white with blackish mouthparts and spiracular plates, and mostly smooth with spiculose intersegmental rings and creeping welts. Cephalopharyngeal skeleton of usual muscoid type; mandible without secondary teeth; discrete dental sclerite lacking; parastomal bar slender; hypopharyngeal sclerite and labial sclerites well-developed; tentoropharyngeal sclerite with more or less equally large dorsal and ventral wings. Anterior spiracle (Fig. 30) with four to twelve digits arranged fan-wise. Terminal segment with three or four pairs of tubercles surrounding spiracular plates (Figs. 31, 32). Posterior spiracles not on raised tubercles; each with three elongate more or less parallel slits.

Biology and behavior. The Piophilidae breed in many kinds of protein-rich plant and animal matter. In the subfamily Neottiophilinae, the larvae of one European species, *Neottiophilum praeustum* (Meigen), are ectoparasitic bloodsuckers on the nestlings of passerine birds. Larvae of most Piophilinae live in animal carrion such as meat, bones, and hides, but larvae of most Mycetaulini, especially *Mycetaulus* and probably *Pseudoceps* and *Amphipogon*, live in rotting fungi. Several species prefer man's environment; the well-known cheese skipper, *Piophila casei* (Linnaeus), is a serious pest in the food industry. Known habits of the Thyreophorina, none of which occur in the Nearctic region, indicate that larvae in this subtribe live in the cadavers of large animals such as dogs, donkeys, horses, monkeys, and humans.

The habit of springing or jumping is well documented for the larva of the cheese skipper, but larvae of other species in the family probably possess a similar ability. The larva first curls up into a C-like form and fastens its mandibles to a fold at its posterior end; by creating muscular tension in the body and suddenly releasing its hold, it then snaps back spring-like to its original elongate form. This action flips the larva into the air and propels it up to several inches at a time.

Classification and distribution. All known genera and species of the world were treated by McAlpine (1977). In that paper the family was redefined to include neottiophilids and thyreophorids and was classified into two subfamilies: the Neottiophilinae, containing one tribe with two genera; and the Piophilinae, containing two tribes, the Mycetaulini with 6 genera and the Piophilini with 14 genera. In all, the family contains 69 described species in 23 genera. Representatives are found on all continents, but the family is richest by far in the temperate and boreal regions of the Northern Hemisphere. Many species of Piophilinae have Holarctic distributions, and a few, such as *P. casei*, are cosmopolitan. Fourteen genera containing about 60 species, a quarter of which are undescribed, occur in the Nearctic region; 11 of these genera are Holarctic.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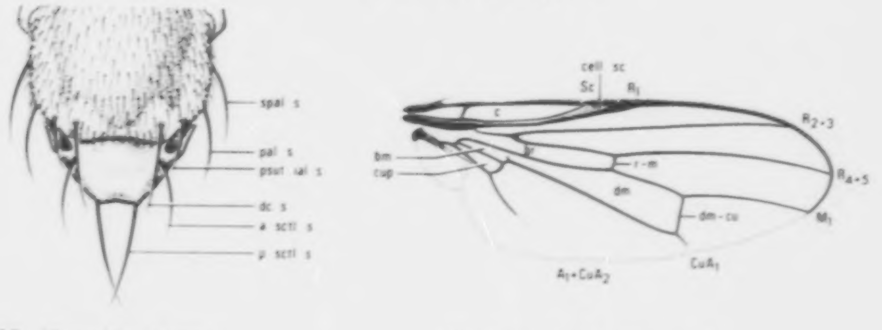
11 Liopiophila varipes ♂

13 Lasiopiophila pilosa ♂

12 Protopiophila latipes ♂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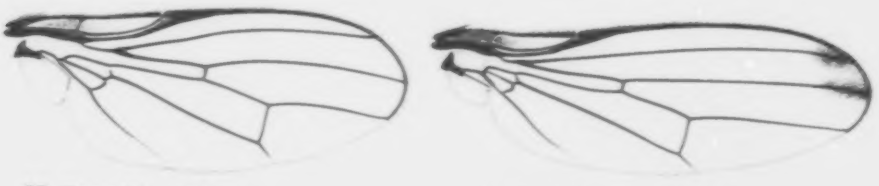
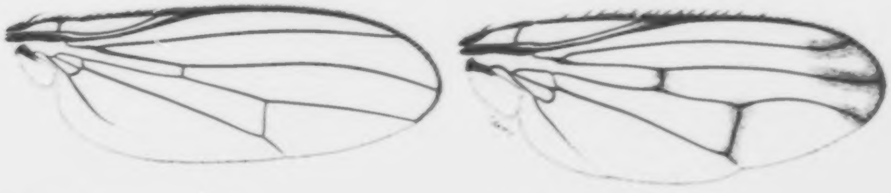
14 Allopiophila luteata ♂

15 Arctopiophila nigerrima ♂



16 Neopiophila setaluna ♀

17 Mycetaulus longipennis ♂

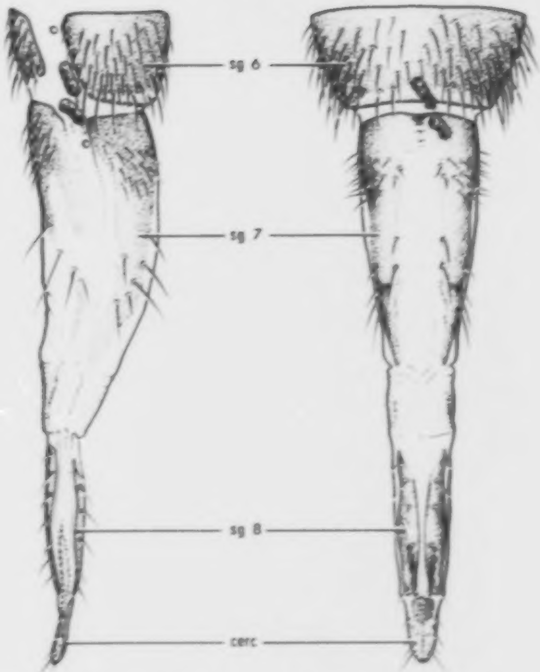


18 Amphipogon hyperboreus ♂

19 Neottiophilum praeustum ♂

Figs. 69.11–19. Thoraces and wings: entire thorax of (11) *Liopiophila varipes* (Meigen) in left lateral view and (12) *Protopiophila latipes* (Meigen) in dorsal view; posterior portion of scutum and scutellum of (13) *Lasiopiophila pilosa* (Staeger) and (14) *Allopiophila luteata* (Haliday) in dorsal view; wings of (15) *Arctopiophila nigerrima* (Lundbeck), (16) *Neopiophila setaluna* McAlpine, (17) *Mycetaulus longipennis* Loew, (18) *Amphipogon hyperboreus* (Greene), and (19) *Neottiophilum praeustum* (Meigen) (Palaearctic).

Abbreviations: anepm, anepimeron; anepst, anepisternum; a sctl s, anterior scutellar seta; dc s, dorsocentral seta; kepst, katepisternum; mr, meron; npl, notopleuron; npl s, notopleural seta; pal s, postalar seta; pprn, postpronotum; pprn s, postpronotal seta; prepst, proepisternum; prepst s, proepisternal seta; presut dc s, presutural dorsocentral seta; presut ial s, presutural intra-alar seta; p sctl s, posterior scutellar seta; psut dc s, postsutural dorsocentral seta; psut ial s, postsutural intra-alar seta; spal s, supra-alar seta.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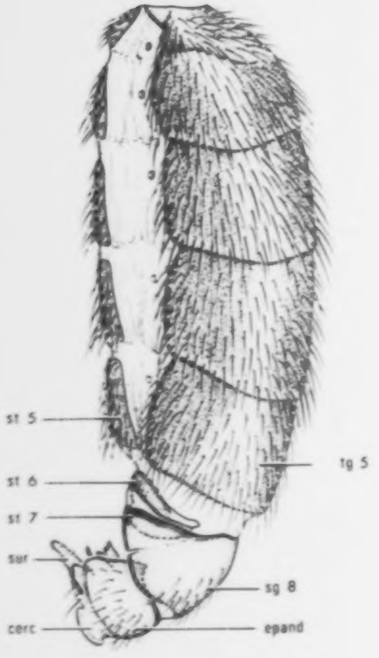
20 Neopiophila setaluna **21** Neopiophila setaluna ♀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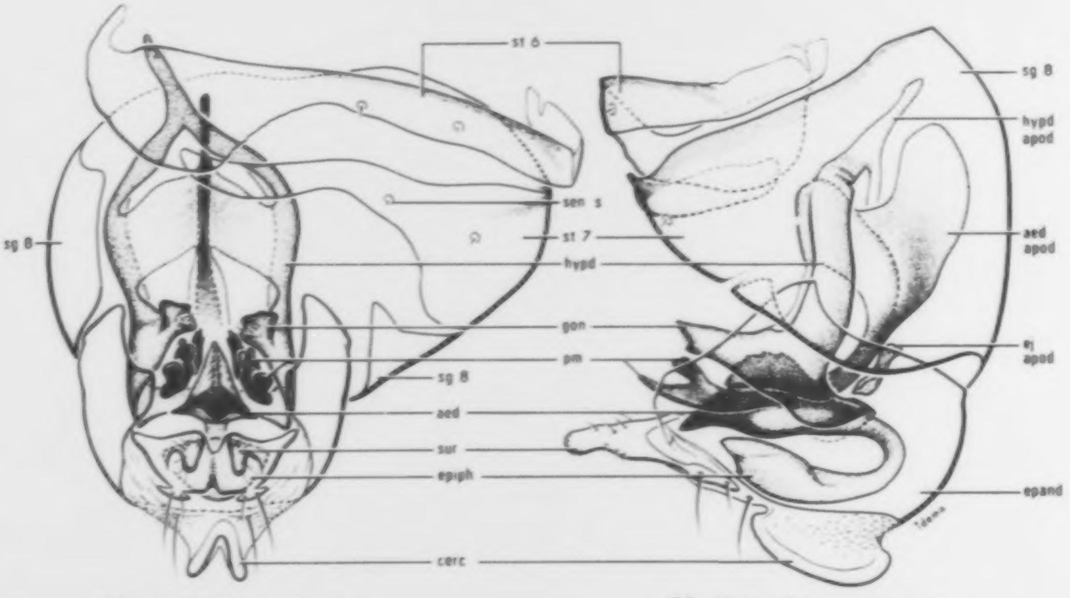
22 Neopiophila setaluna ♂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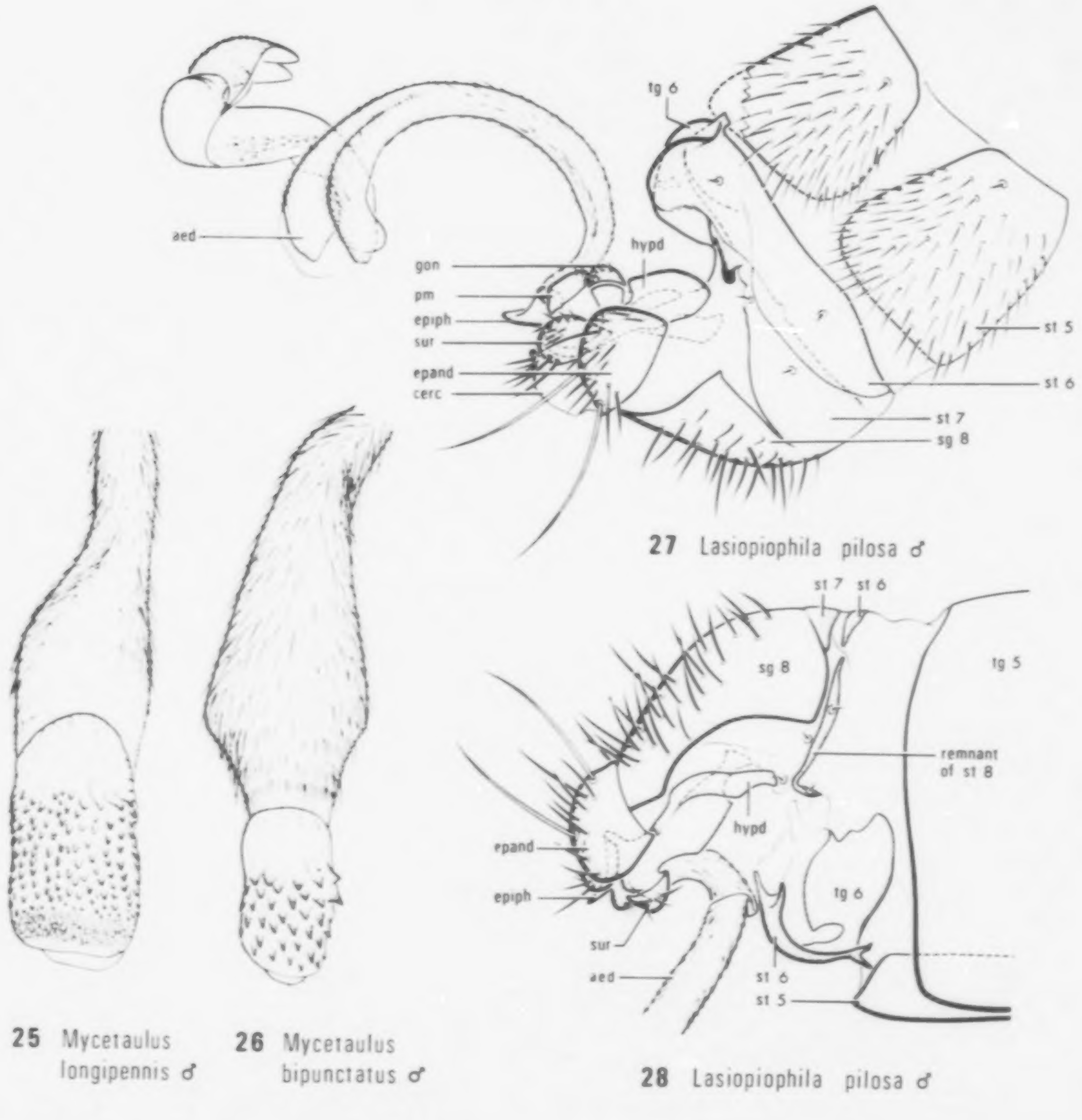
23 Neopiophila setaluna ♂ **24** Neopiophila setaluna ♂

Figs. 69.20–24. Terminalia of *Neopiophila setaluna* McAlpine: (20, 21) ovipositor, left lateral and dorsal views; (22) entire abdomen of male with terminalia exposed, left lateral view; (23, 24) details of male terminalia, ventral and left lateral views.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; hypd apod, hypandrial apodeme; pm, paramere; sen s, sensory setula; sg, segment; st, sternite; sur, surstylus; tg, tergite.



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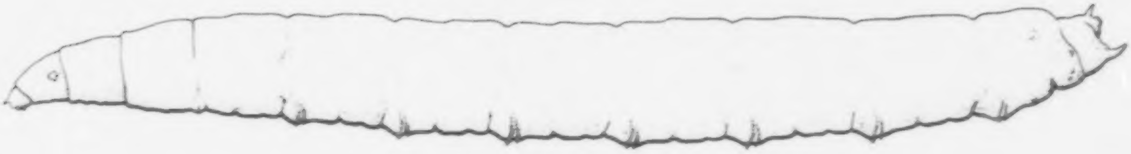
27 Lasiopiophila pilosa ♂

25 Mycetaulus longipennis ♂

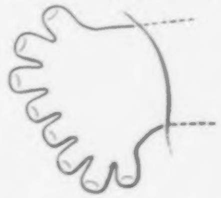
26 Mycetaulus bipunctatus ♂

28 Lasiopiophila pilosa ♂

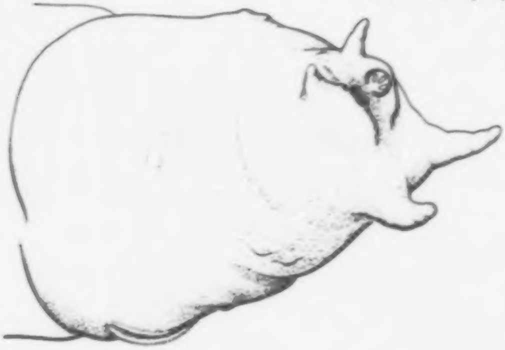
Figs. 69.25–28. Male terminalia: dorsal views of apical glans of aedeagus of (25) *Mycetaulus longipennis* Loew and (26) *M. bipunctatus* (Fallén) (Palaearctic); (27) left lateral and (28) right lateral views of *Lasiopiophila pilosa* (Staeger).
Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; pm, paramere; sg, segment; st, sternite; sur, surstylus; tg, tergite.



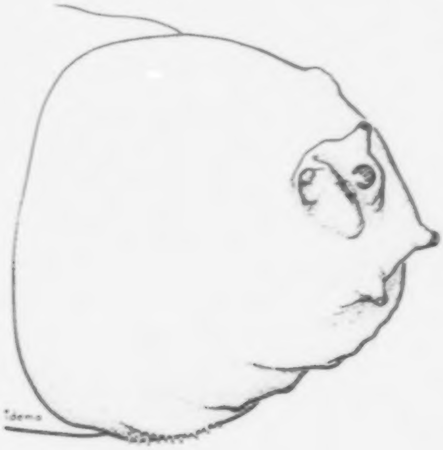
29 Lasiopiophila pilosa



30 Lasiopiophila pilosa



31 Lasiopiophila pilosa



32 Arctopiophila arctica

Figs. 69.29–32. Larvae: (29) *Lasiopiophila pilosa* (Staeger), left lateral view; (30) anterior spiracle of *L. pilosa*; (31) apical portion of abdomen of *L. pilosa*; (32) apical portion of abdomen of *Arctopiophila arctica* (Holmgren).

Key to genera

1. R_1 setulose above (as in Fig. 19) . . . . NEOTTIOPHILINAE . . . . ***Actenoptera*** Czerny
   2 spp.; McAlpine 1977

   R_1 bare (Figs. 15–18) . . . . PIOPHILINAE 2

2. Scutellum with two wart-like tubercles apically, and with a few hairs in addition to usual four bristles (Fig. 13). Extensively hairy pruinose species, with strong postpronotal bristle and setulose anepisternum . . . . ***Lasiopiophila*** Duda
   1 sp., *pilosa* (Staeger); Holarctic

   Scutellum without wart-like tubercles (Figs. 12, 14), with four bristles only, except in *Neopiophila*. Other characters applicable or not 3

3. Postpronotal and presutural intra-alar bristles absent (Fig. 11) 4

   Postpronotal and usually presutural intra-alar bristles present (Fig. 12) 7

4. Anepisternum bare; anterior convex portion of anepimeron bare and polished. Ocellar (Fig. 2) and proepisternal bristles weak . . . . ***Stearibia*** Lioy
   1 sp., *nigriceps* (Meigen); Holarctic

Anepisternum setulose (Fig. 11); anterior portion of anepimeron with or without setulae or pruinescence. Ocellar and proepisternal bristles weak to strong 5

5. Anepimeron setulose (Fig. 11) .... ***Liopiophila*** Duda
1 sp., *varipes* (Meigen); Holarctic

Anepimeron not setulose 6

6. Dorsocentral rows of setulae differentiated from mesonotal hairs (Fig. 1); pleural hairs and bristles black; proepisternal bristle fairly strong (Fig. 1) .... ***Piophila*** Fallén
1 sp., *casei* (Linnaeus); cosmopolitan

Dorsocentral rows of setulae indistinguishable from mesonotal hairs (as in Figs. 12–14); pleural hairs and bristles whitish; proepisternal bristle rather weak .... ***Prochyliza*** Walker
5 spp.; McAlpine 1977

7. Postpronotum with two bristles, the inner one incurved (Fig. 12); one presutural dorsocentral bristle present (Fig. 12), sometimes scarcely distinguishable .... ***Protopiophila*** Duda
1 sp., *latipes* (Meigen); Holarctic

Postpronotum with one bristle, the inner one absent; presutural dorsocentral bristle absent 8

8. One postsutural dorsocentral bristle present (Fig. 14). Wing almost always without markings 9

Two or more postsutural dorsocentral bristles present. Wing usually with markings (Figs. 16–18) 13

9. Prosternum setulose 10

Prosternum bare 11

10. Lunule setulose; palpus enlarged (Fig. 4). Scutellum hairy. Costal and subcostal cells fumose (Fig. 16) .... ***Neopiophila*** McAlpine
1 sp., *setaluna* McAlpine; Canadian Arctic

Lunule bare; palpus normal (Fig. 3). Scutellum with four bristles only (Fig. 14). Only subcostal cell fumose .... ***Allopiophila*** Hendel
1 sp., *luteata* (Haliday); Holarctic

11. Subcostal section of C long, at least as long as width of cell c (Fig. 15). Head, including antennae and palpi, black. Halter blackish .... ***Arctopiophila*** Duda
2 spp.; Holarctic; McAlpine 1977

Subcostal section of C shorter, not as long as greatest width of cell c (Figs. 17, 18). Head, antennae, and palpi (or some combination) with some yellow coloration. Halter white 12

12. Thorax and abdomen entirely grayish pruinose .... ***Boreopiophila*** Frey
1 sp., *tomentosa* Frey; Holarctic

Thorax and abdomen mostly polished black .... ***Parapiophila*** McAlpine
about 20 spp.; McAlpine 1977

13. Head as long as high (Fig. 6). Wing without an apical spot (Fig. 18). Male grotesquely decorated on head (Fig. 6), legs, and terminalia .... ***Amphipogon*** Wahlberg
1 sp., *hyperboreus* (Greene); northwestern

Head shorter than high (Fig. 5). Wing usually with an apical spot (Fig. 17). Not sexually dimorphic .... ***Mycetaulus*** Loew
many species; McAlpine 1977

Reference

McAlpine, J. F. 1977. A revised classification of the Piophilidae including 'Neottiophilidae' and 'Thyriophoridae' (Diptera: Schizophora). Mem. Can. Ent. 103: 1–66.

CLUSIIDAE

70

Á. Soós

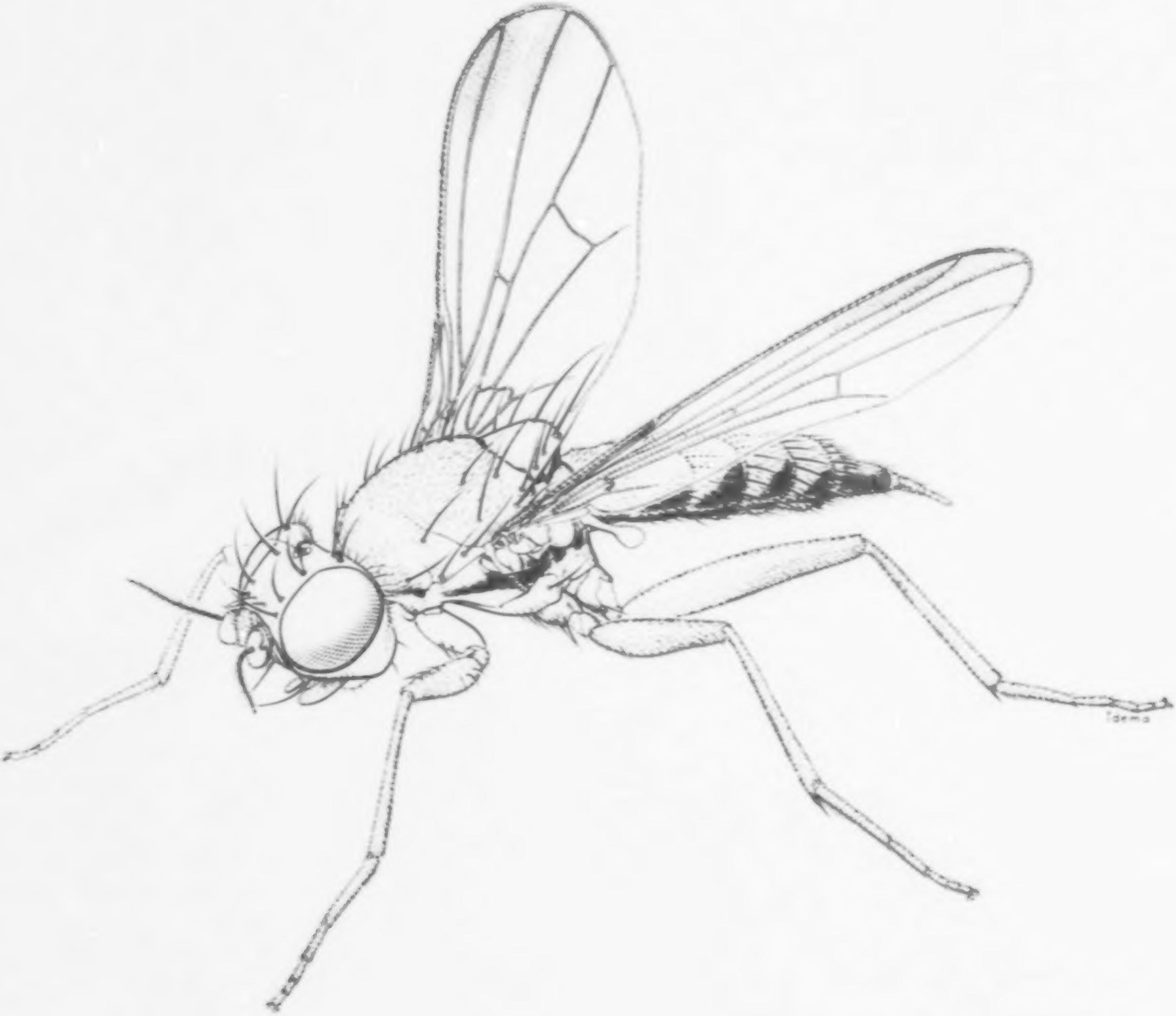


Fig. 70.1. Adult female of *Clusia lateralis* (Walker).

Slender flies (Fig. 1), 1.8–7.5 mm long, yellow to black, ornamented with markings of various size and shape, dull to shining, rarely pruinose. Wing fumous hyaline, frequently with apices variably clouded, and sometimes more extensively marked.

Adult. Head: almost invariably higher than long, rarely only as high as long, and always wider than high (Figs. 2, 3). Eye bare or pubescent. Postcranium concave on upper half to entirely flat. Frons weakly sclerotized, slightly depressed, usually longer than wide, but frequently as wide as long to considerably wider than long; sides of frons usually nearly parallel, but sometimes strikingly narrowed anteriorly and, more rarely, posteriorly; lunule usually covered, but exposed in *Clusiodes* Coquillett (Fig. 2). Middle of face soft, sclerotized only in its upper part between antennae, and usually more depressed than parafacials; facial carina absent; cuticle in this region soft and unsclerotized. Clypeus more or less prominent; gena generally narrow, in middle region about one-fifth to one-ninth height of eye; postgenal region ventrally prominent. Antenna decumbent or porrect, usually short; bases usually closely adjacent, rarely with distance between them greater than that between base of antenna and margin of eye; pedicel and first flagellomere rarely distinctly elongated; scape extremely small; pedicel usually with a very characteristic triangular extension on outer side and a long terminal to subterminal dorsal bristle (Figs. 2, 3, 2.42); first flagellomere usually orbicular or discoid, rarely elongated; arista usually with loose to dense hairs of varying size, rarely smooth or microscopically pubescent. Postocellar bristles present or absent; when present these divergent, arising close to one another and to ocellar bristles, never robust, and always considerably weaker and shorter than vertical bristles; ocellar bristles short, usually about as long as postocellar ones; about 10–15 postocular setulae present on either side of inner vertical bristles, with upper ones directed upward and lower ones downward; vertical bristles always well-developed, with inner ones always longer than outer ones. Fronto-orbital plates more or less continuous from vertex to parafacial; orbital plate not distinct from frontal plate; sometimes a series of several to many tiny setulae present laterally to main row of fronto-orbital bristles. Two to five fronto-orbital bristles present; sometimes lowermost one (possibly a true frontal bristle) inclinate and slightly proclinate and all others reclinate (Clusiinae) (Figs. 1, 3); sometimes all fronto-orbital bristles reclinate (Fig. 2), or occasionally the second or third pair, but never the uppermost pair (first pair), inclinate (Clusiodinae). Interfrontal bristles present (Fig. 2) or absent (Fig. 3); when present their length as well as their position in relation to each other and to ptilinal suture highly variable; interfrontal area with or without additional tiny setulae. Vibrissae invariably well-developed, usually directed forward and upward; two to eight subvibrissal bristles, varying in length and strength, present below and behind vibrissae; one or two posteroventrally directed genal bristles present (Fig. 3).

Thorax: usually 1.5–2.0 times as long as wide, and usually as wide as head. Chaetotaxy: one postpronotal, two notopleural, zero to two presutural supra-alar, one to four postsutural supra-alar, one or two postalar, zero postsutural intra-alar, zero or one prescutellar acrostichal, and zero or one presutural and one to three postsutural dorsocentral bristles present; scutellum smooth, with one pair of subapical and one or two pairs of lateral bristles; thorax laterally with zero to two proepisternal, one anepisternal, and one katepisternal bristle present. Prosternum usually, if not always, setulose.

Wing (Fig. 6) usually at least twice as long as wide, with apex widely rounded. C usually reaching M_1, with subcostal break only (absent in some *Clusiodes* spp.); Sc well-developed, attaining C, and parallel with R_1; R_1 occasionally setulose above; crossveins r-m and dm-cu frequently closely approaching one another, but this character widely variable; ratio of penultimate to ultimate sections of M usually a good specific or species-group feature; cells bm and cu*p* complete; A_1 well-developed, but not attaining wing margin.

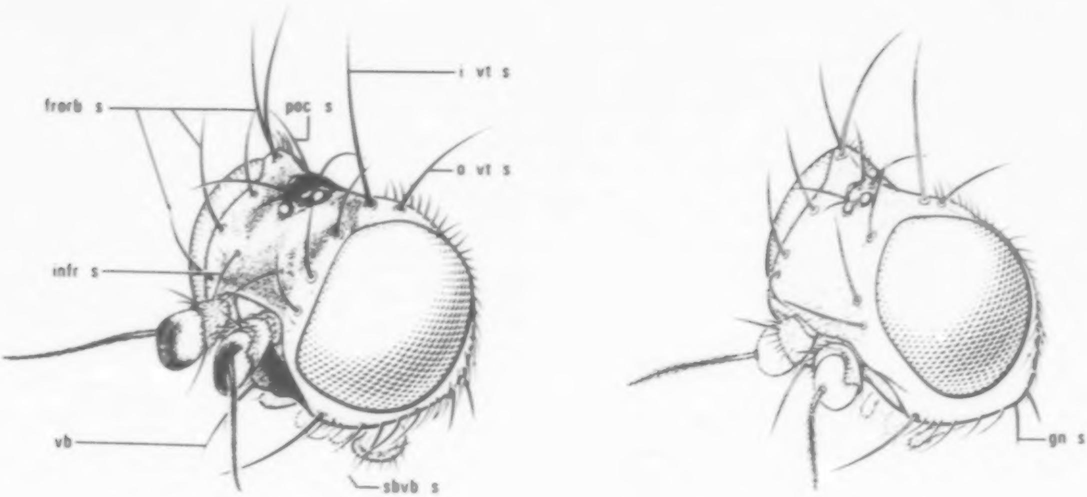
Legs moderately setulose. Fore and middle femora of male usually with numerous stronger posteroventral and some shorter anteroventral bristles; female without well-developed femoral bristles. Tibiae (Figs. 4, 5), except for *Heteromeringia* Czerny (Fig. 5) and *Allometopon* Kertész (latter not Nearctic), with well-developed preapical dorsal bristles at least on middle tibia (Fig. 4).

Abdomen: fairly slender and pointed (Fig. 1). Male terminalia very characteristic (Figs. 8, 9). Tergite 6 well-developed, symmetric, with one pair of spiracles (sixth) below its lateral margins; sternite 6 shifted to left side, and usually in contact with sternite 7. Sternite 7 situated still higher on left side, adjacent to or connected with large dorsal sclerite of segment 8; seventh spiracle on left side enclosed in suture line between sternites 7 and 8, with the right one in membrane on the right side; sternites 6–8 sometimes fused into a complete annulus (*Clusiodes* Coquillett). Segment 9 deflexed and symmetric; epandrium (Fig. 9) large and bearing one or two pairs of surstylar processes; surstyli articulated with ventral margin of epandrium, each forming one or two surstylar processes of varying shapes; hypandrium (Fig. 8) smaller and with either a concave ventral surface or with a desclerotized central and posterior region into which base of aedeagus can be folded; gonopods usually closely associated with sides of hypandrium; parameres small, but frequently bilobate; aedeagus borne on posterior part of sternite 9, variable in structure, comprising a sclerotized basiphallus and a membranous distiphallus; basiphallus usually short, with or without one or two pairs of anterior processes, and with a median posterior epiphallus; distiphallus varying in length, often long and coiled in repose and branching distally, and in *Heteromeringia* with a rather distinct apical glans supported by a pair of longitudinal skeletal strips. Cerci usually present in membranous region surrounding anus (D. K. McAlpine 1960).

Female with abdominal tergites and sternites 1–7 well-developed; those of segments 7 and 8 not fused laterally (Fig. 10). Segment 8 very slender, elongate, separated from segment 7 by an extensive membrane. Hypoproct and epiproct closely associated at base. Cerci elongate (Fig. 11), often with two or three outstanding bristles at distal end. Seven pairs of spiracles present. Two sclerotized spermathecae present, broadly ovate (Fig. 10).

Larva. Those few known slender, subcylindrical, unpigmented except on posterior spiracular process (Fig. 7, puparium). Head with mandibles small but well-sclerotized; cephalopharyngeal skeleton vestigial, unpigmented.

Body smooth, except for very small locomotor spinules arranged on middle of sternites and anterior margins of tergites. Anterior spiracles each on a small tubercle, and each with three to six openings. Posterior spiracles (Fig. 7, puparium) somewhat elevated, situated on inner surface of distinctly separated or undivided plates; plates sclerotized, large, and flat, bearing paired terminal upwardly curving conical processes; each spiracle with three short oval irregularly arranged slit-like openings.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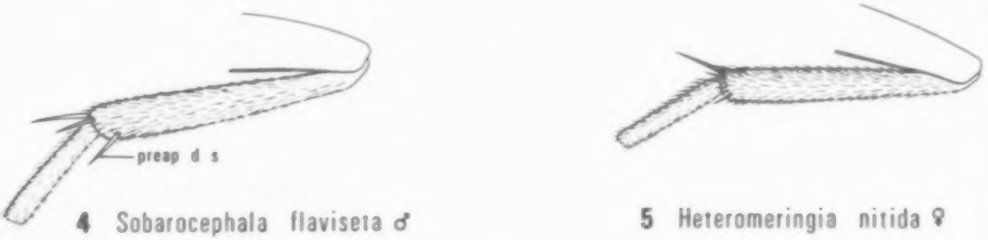
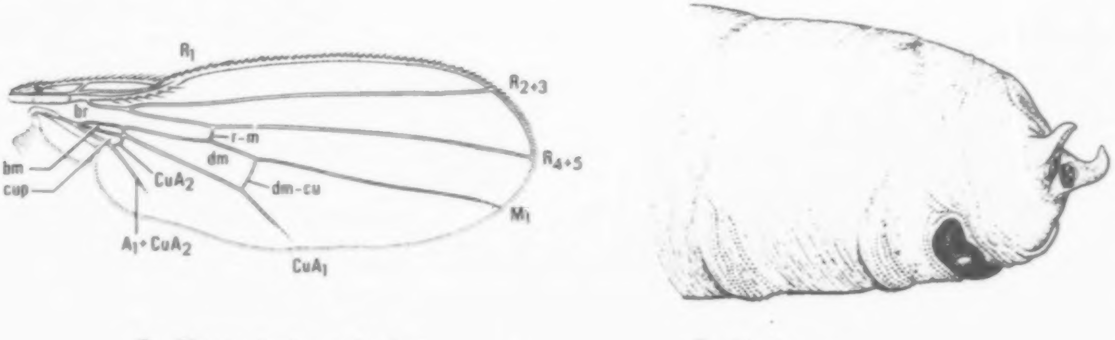
2 Clusiodes albimanus ♀ 3 Sobarocephala flaviseta ♂



4 Sobarocephala flaviseta ♂ 5 Heteromeringia nitida ♀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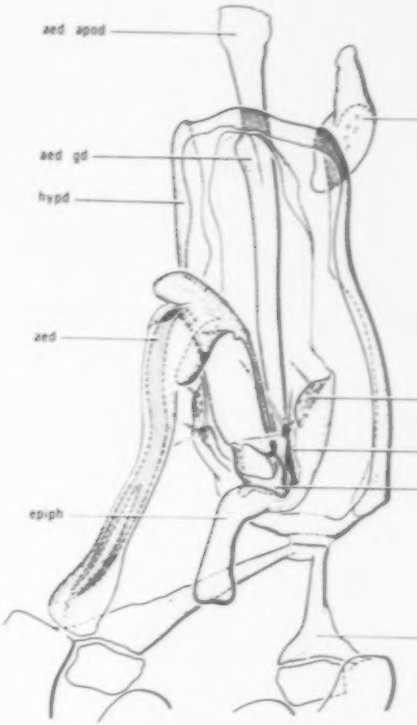
CuA_1

6 Chaetoclusia bakeri ♂ 7 Clusia sp.

Figs. 70.2–7. Heads, mid tibiae, wing, and puparium: head of (2) *Clusiodes albimanus* (Meigen) and (3) *Sobarocephala flaviseta* (Johnson); left mid tibia of (4) *S. flaviseta* and (5) *Heteromeringia nitida* Johnson in anterior view; (6) wing of *Chaetoclusia bakeri* Coquillett (Neotropical); (7) terminal portion of puparium of *Clusia* sp., left posterolateral view.

Abbreviations: frorb s, fronto-orbital bristle; gn s, genal bristle; infr s, interfrontal bristle; i vt s, inner vertical bristle; o vt s, outer vertical bristle; poc s, postocellar bristle; preap d s, preapical dorsal bristle; sbvb s, subvibrissal bristle; vb, vibrissa.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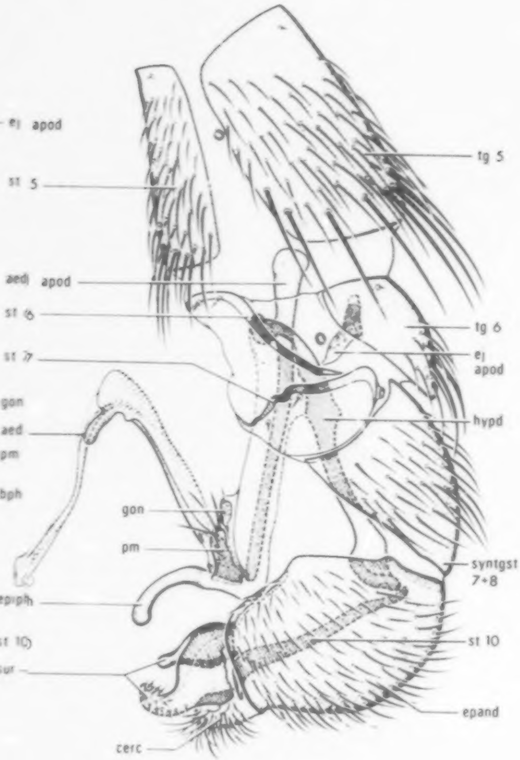
8 Clusia lateralis ♂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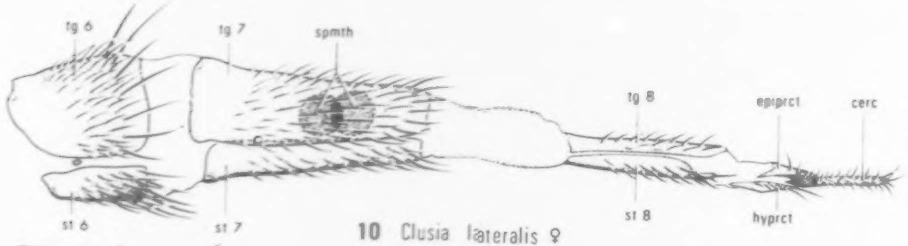
9 Clusia lateralis ♂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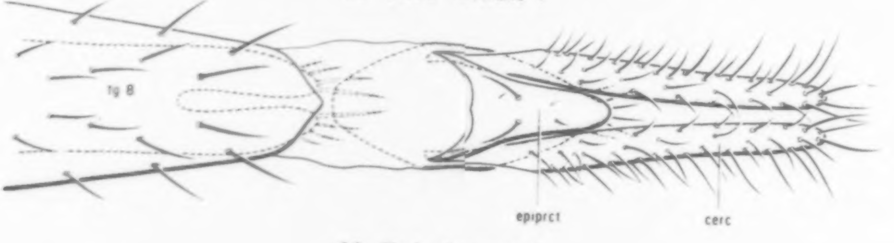
10 Clusia lateralis ♀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11 Clusia lateralis ♀

Figs. 70.8–11. Terminalia: (8) hypandrium and associated parts of *Clusia lateralis* (Walker), ventral view; (9) male terminalia of *C. lateralis*, left lateral view; (10) female terminalia of *C. lateralis*, left lateral view; and (11) apex of ovipositor of *C. lateralis*, dorsal view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; bph, basiphallus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

Biology and behavior. Known larvae live in rotting wood and termite galleries. The adults usually occur around decaying tree trunks and are fairly commonly found on windows. They feed on nectar, rotting vegetable matter, or sap.

Classification and distribution. At present 25 genera, 217 species, and 6 subspecies of the family are known. They occur in all parts of the world except the polar regions. Four genera and 35 species are known from the Nearctic region. Two fossil species, *Electroclusiodes meunieri* (Hendel) and *Electroclusiodes radiospinosa* Hennig are described from Baltic amber (Hennig 1965, 1969). Also, see remarks about *Acartophthalmites tertiariae* Hennig under classification and distribution of Acartophthalmidae, Chapter 71.

Key to genera

1. All fronto-orbital bristles reclinate; lunule exposed; interfrontal bristles present, inserted considerably above ptilinal suture (Fig. 2). Preapical dorsal tibial bristles well-developed (as in Fig. 4) .... CLUSIODINAE .... ***Clusiodes*** Coquillett
14 spp.; widespread; Melander and Argo 1924

Lower pair of fronto-orbital bristles medioclinate or proclinate, and others reclinate; lunule covered (Fig. 3); interfrontal bristles usually absent, rarely present *(Clusia)*. Preapical dorsal tibial bristles present (Fig. 4) or absent .... CLUSIINAE 2

2. Interfrontal bristles present (as in Fig. 2). Preapical dorsal tibial bristles vestigial (as in Fig. 5). Postocellar and prescutellar acrostichal bristles absent; proepisternal bristle long; presutural supra-alar bristle present (Fig. 1). Adult 5–7.5 mm long .... ***Clusia*** Haliday
3 spp.; 2 eastern, 1 western; Melander and Argo 1924

Interfrontal bristles absent (Fig. 3). Preapical dorsal tibial bristles variable. Presutural supra-alar bristles absent. Adult 3–5 mm long 3

3. R_1 setulose above (Fig. 6). Postocellar and proepisternal bristles absent. Preapical dorsal tibial bristle present on mid tibia (as in Fig. 4) .... ***Chaetoclusia*** Coquillett
1 sp., *affinis* Johnson[1]; New Jersey; Melander and Argo 1924

R_1 not setulose. Postocellar bristles present. Preapical dorsal tibial bristles variable 4

4. Preapical dorsal tibial bristles well-developed, at least on middle tibia (Fig. 4) .... ***Sobarocephala*** Czerny
14 spp.; mainly eastern North America; Melander and Argo 1924, Soós 1963, Sabrosky and Steyskal 1974

Preapical dorsal tibial bristle weak or absent on all tibiae .... ***Heteromeringia*** Czerny
3 spp.; widespread; Melander and Argo 1924

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[1] Now recognized as an additional species of *Sobarocephala* and junior synonym of *S. testacea* Soós (see Woodley 1984).

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ACARTOPHTHALMIDAE

71

J. F. McALPINE

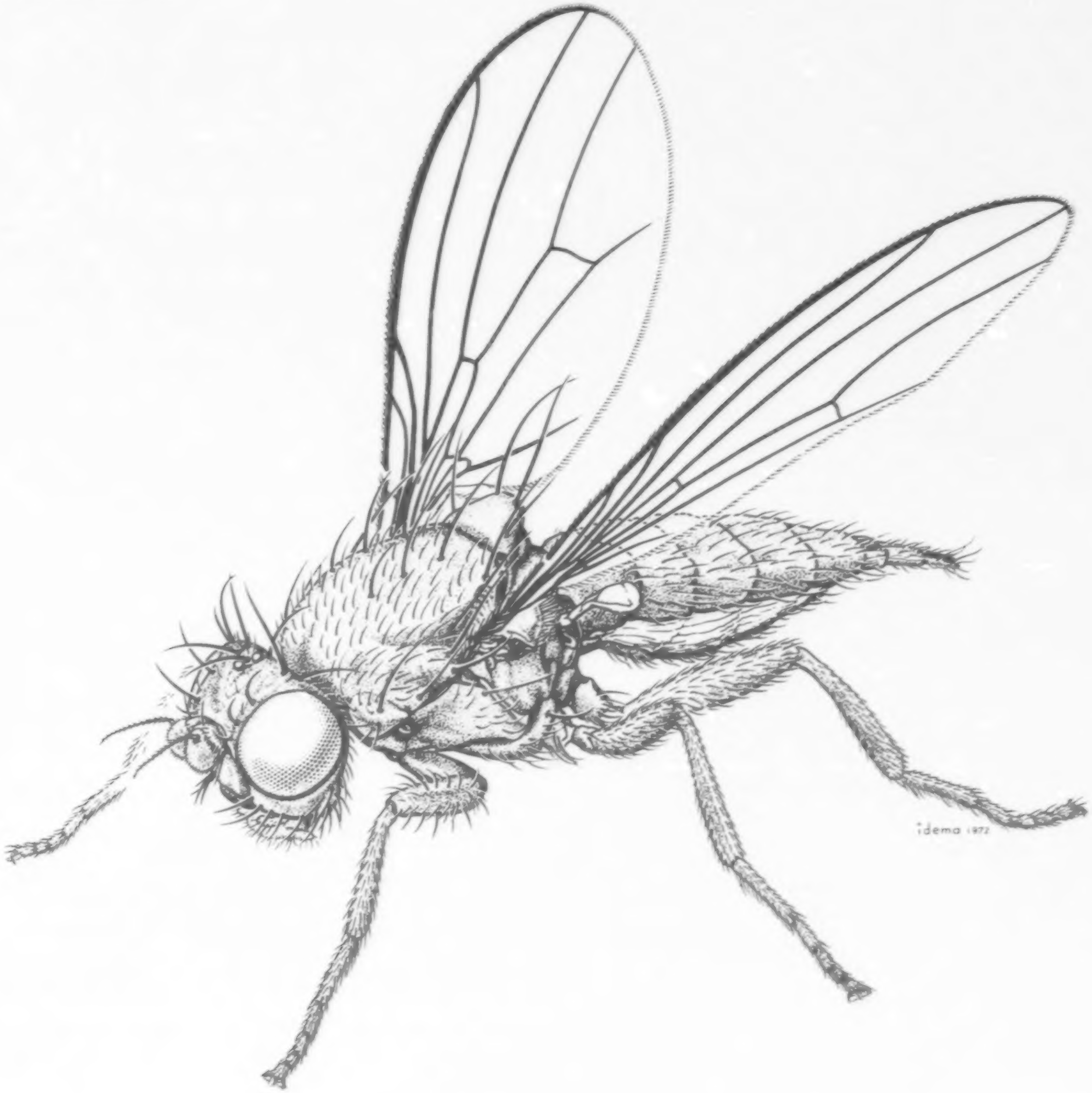
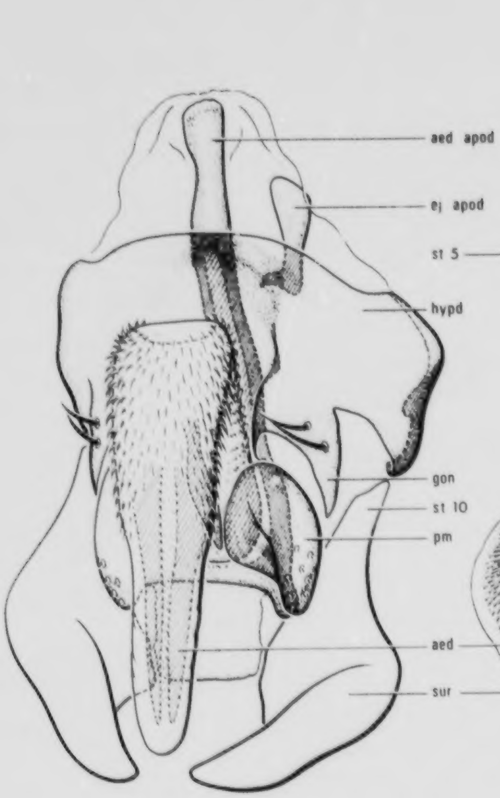


Fig. 71.1. Adult female of *Acartophthalmus nigrinus* (Zetterstedt).

Very small drosophilid-like flies (Fig. 1), 2.5–3.0 mm long, dull brownish gray in color, with slightly fumose wings. Only two extant species known, both Holarctic.

Adult. Head: higher than long, strongly bristled (Fig. 1). Compound eye nearly round, distinctly pubescent. Frons strongly narrowed from vertex to lunule; fronto-orbital plate very narrow, scarcely differentiated from remainder of frons; three pairs of evenly spaced lateroreclinate fronto-orbital bristles present; uppermost pair strongest and arising opposite anterior ocellus; lowermost pair weakest and arising at upper level of ptilinal suture; ocellar, inner and outer vertical, and postocellar bristles subequal in length and strength; postocellar bristles widely spaced, strongly divergent, arising behind and slightly lateral to posterior ocelli. Gena narrower than width of first flagellomere, with a row of four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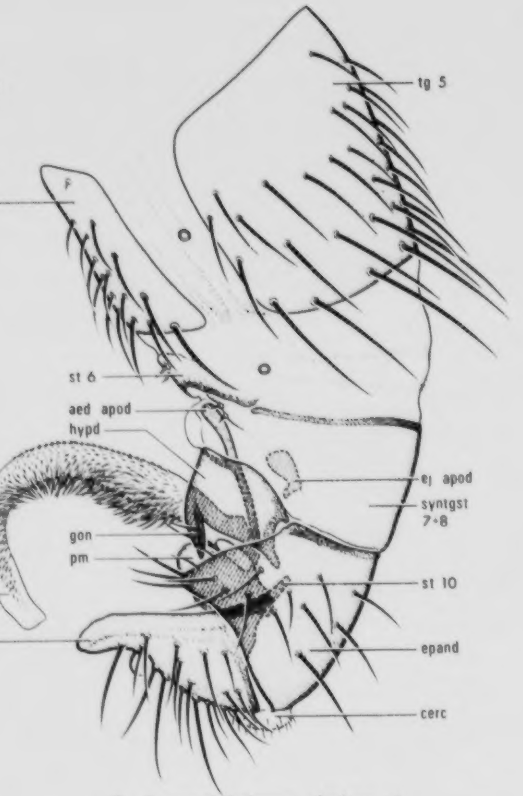
2 Acartophthalmus nigrinus ♂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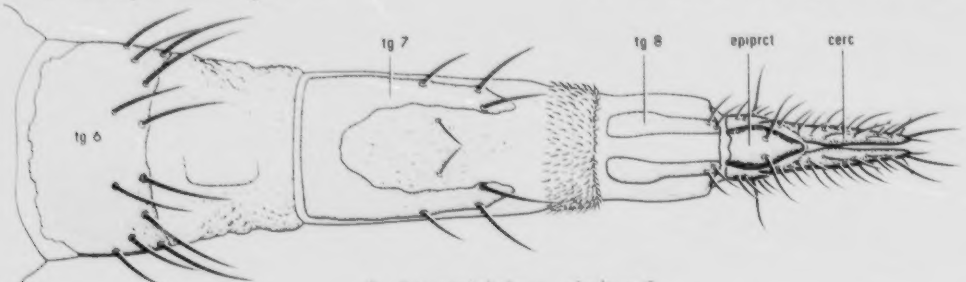
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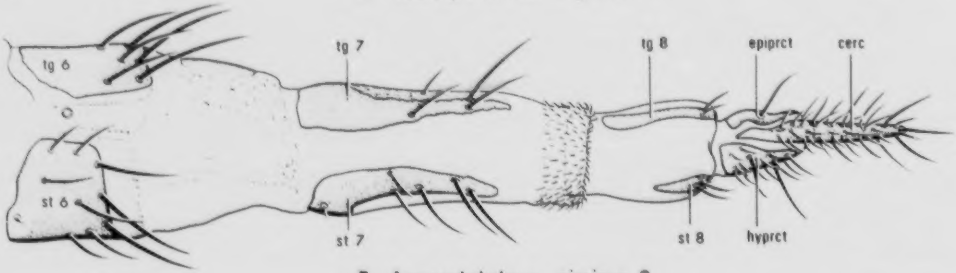
4 Acartophthalmus nigrinus ♀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5 Acartophthalmus nigrinus ♀

Figs. 71.2–5. Terminalia of *Acartophthalmus nigrinus* (Zetterstedt): (2) hypandrium, ventral view; (3) male terminalia, left lateral view; (4) dorsal and (5) left lateral views of female terminalia.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

or five relatively strongly developed subvibrissal setae; anteriormost one, the vibrissa, scarcely larger or otherwise distinguishable from others. Face depressed, with a membranous furrow extending from clypeus to lunule. Antenna short; pedicel short and simple, slightly angular on outer distal margin; first flagellomere orbicular; arista arising on basal third, shortly pubescent. Mouthparts and palpus normal.

Thorax: scutum uniformly dull brownish gray; prescutellum absent. Chaetotaxy: scutum setulose throughout (Fig. 1); one postpronotal bristle present; presutural supra-alar bristle absent; presutural dorsocentral bristles absent; three or four postsutural dorsocentral bristles present; two postalar bristles present, the inner one very weak; postsutural intra-alar and prescutellar acrostichal bristles absent or indistinct; scutellum with two pairs of bristles only; two notopleural bristles present; proepisternal and proepimeral bristles absent; anepisternum and katepisternum each with one bristle and numerous setulae; pleural sclerites otherwise bare. Prosternum fairly broad, free at sides, bare. Wing at least twice as long as broad, with well-developed anal lobe and alula; C extending weakly to M_1, with humeral break only just beyond crossvein h, without outstanding costal spines; Sc complete, joining C far before insertion of R_1; cells dm and bm separated by crossvein; cell cu*p* present; A_1 not attaining wing margin. Legs unmodified, weakly bristled; preapical dorsal tibial bristles absent or indistinct.

Abdomen: more or less cylindrical (Fig. 1); segments 1–5 unmodified in both sexes; six pairs of spiracles in both sexes.

Male (Figs. 2, 3) with sternites 6–8 fused, forming a bare ring-like pregenital segment which is nearly symmetric on dorsum and nearly as long as epandrium. Epandrium uniformly setulose, roughly triangular in side view, with a lateroventral point lying in front of base of surstylus; surstylus relatively large, pendulant, freely articulating with ventral margin of epandrium, setulose but without coarse teeth. Hypandrium open posteriorly, without hypandrial bridge behind basiphallus; gonopods and parameres small and simple; aedeagus membranous, stout at base and tapering to relatively slender apex, without epiphallus, pubescent throughout; apical portion of aedeagus stored in membranous area on left side of abdomen between epandrium and sternites 6–7; aedeagal apodeme rod-like, rather short. Cerci very small and membranous.

Female (Figs. 4,5) with tergite 7 and sternite 7 free from each other. Tergite 8 and sternite 8 completely divided along midline; cerci elongate, free from each other. Spermathecae indiscernible.

Biology and behavior. The immature stages are unknown. Adults frequent rotting fungi in damp woods. Their wings are strongly irridescent, and males, especially, are sometimes observed flicking their wings up and down in otitid-like fashion around fungi on logs, stumps, and decaying organic matter.

Classification and distribution. The family, formerly placed as a subfamily of the Clusiidae, consists of one genus, *Acartophthalmus* Czerny; two Holarctic species, *A. nigrinus* (Zetterstedt) (type of genus) and *A. bicolor* Oldenberg are assigned to it. The most recent treatments of these species are by Melander and Argo (1924), Czerny (1928), and Frey (1946).

One fossil species, *Acartophthalmites tertiariae* Hennig, described from Baltic amber (Hennig 1965, 1969), was questionably assigned to the Acartophthalmidae. It differs from recent *Acartophthalmus* species in the following characters: size larger (4–4.5 mm), thorax with brown stripes, eye bare, gena broader, postocellar bristles closer together, outer side of pedicel with stronger distal projection, arista with longer pubescence, prescutellar acrostichal bristles present, prosternum with four tiny hairs on each side (at least in specimen in Mus. Comp. Zool. Cambridge, Hennig 1969 notwithstanding), R_1 bristled on apical half, subcostal break weakly present (at least in specimen in Mus. Comp. Zool. Cambridge, Hennig 1969 notwithstanding), humeral costal break absent, A_1 longer, and proepisternal bristle present. In all these characters it agrees with certain Clusiidae, especially those in which R_1 is bristled, i.e. *Trichoclusia* Soós (Cuba), *Chaetoclusiella* Soós (Brazil), and *Chaetoclusia* Coquillet (Central America). It is most probably a clusiid rather than an acartophthalmid.

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ODINIIDAE

72

J. F. McAlpine

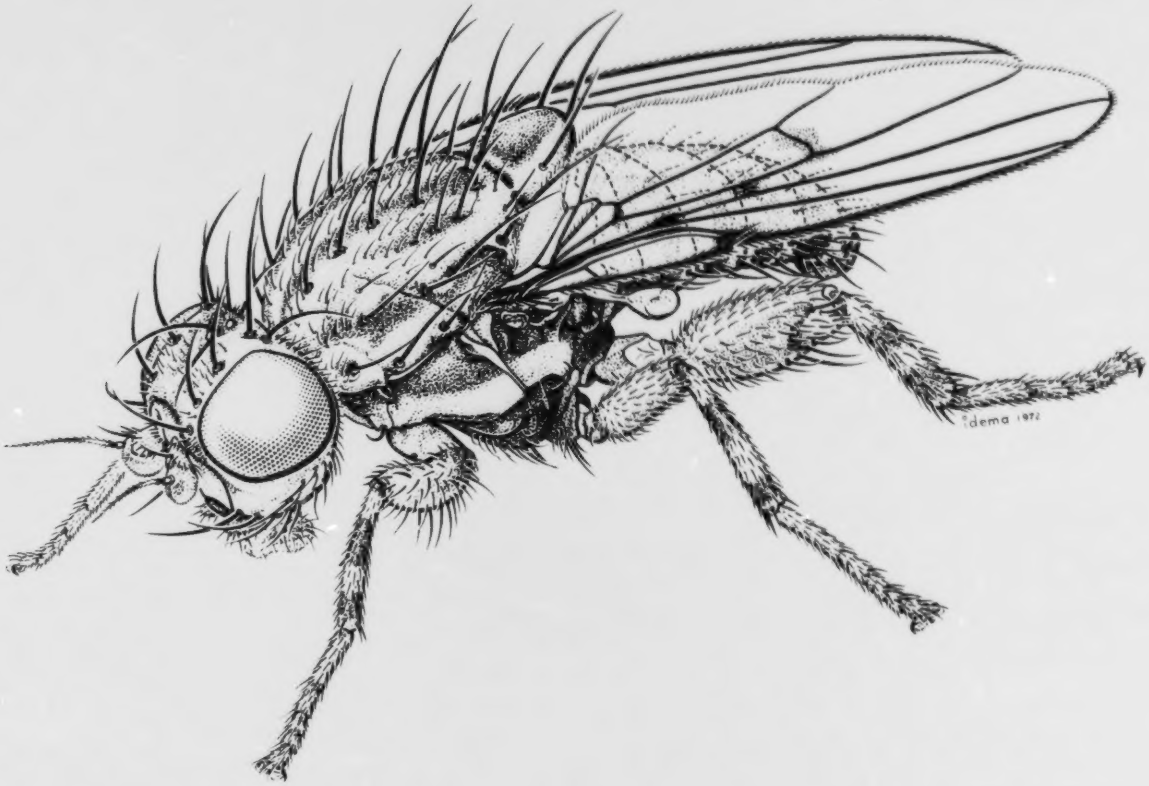


Fig. 72.1. Male of *Odinia betulae* Sabrosky.

Small, compact, strongly bristled flies (Fig.1), 3–4 mm long; body dull gray, with brown markings; legs stout, with banded tibiae; wings with few to many brownish spots, always darkened around subcostal break in Nearctic species.

Adult. Head: about as broad as thorax, distinctly higher than long (Fig. 2). Frons nearly as broad as long, of same width in both sexes, slightly narrower at lunule than at vertex; interfrontal area very sparsely and finely setulose; fronto-orbital plate more or less continuous from vertex to lunule; ocellar plate normal (*Odinia* Robineau-Desvoidy, Fig. 1, and *Neoalticomerus* Hendel) to unusually prominent (*Traginops* Coquillett, Fig. 2). Inner vertical bristle usually stronger than outer vertical; postocellar bristles strongly divergent; ocellar bristles arising on margins of ocellar plate distinctly posteriorly to (above) anterior ocellus; fronto-orbital plate with two reclinate bristles above and one medioreclinate bristle below (Figs. 1, 2); lunule broadly exposed, bare. Face somewhat concave, bare, uniformly sclerotized; median carina weak to absent; parafacial sublinear. Clypeus small and withdrawn (*Odinia*, Fig. 1, and *Neoalticomerus)* to relatively large and prominent (*Traginops*, Fig. 2); cheek rather broad; vibrissa strong; subvibrissal bristles decreasing in size posteriorly; gena with one to several genal bristles and numerous subvibrissal setulae. Compound eye nearly round to somewhat horizontally oval, bare. Antenna short and porrect, usually predominantly orange yellow; scape very short, with few fine setulae; pedicel shallowly notched on dorsal margin, with numerous fine marginal setulae and a bristle near margin of inner dorsal surface; first flagellomere about as broad as long, with rounded apex; arista shortly pubescent (plumose in some exotic forms). Proboscis short, with well-developed labella; palpus relatively large, somewhat flattened, frequently at least partly orange yellow, with numerous black setulae.

Thorax: brownish in ground color, patterned with dense gray and brown pruinescence. Scutum rather short and broad, not strongly arched; prescutellum present (*Odinia* and *Neoalticomerus*) or absent (*Traginops*); scutellum large, with convex disc; subscutellum moderately well-developed. Chaetotaxy: one (*Odinia* and *Neoalticomerus*) or three postpronotal bristles (*Traginops*), one presutural and three or four postsutural dorsocentral bristles, one prescutellar acrostichal bristle, one to several postsutural intra-alar bristles, one postsutural supra-alar bristle, two postalar bristles, and one lateral and one subapical scutellar bristle present; disc with (*Traginops*) or without (*Odinia* and *Neoalticomerus*) discal setulae; notopleuron with two bristles; propleuron bare on disc; one proepisternal bristle present; proepimeral bristle absent in Nearctic genera (bristled in *Neotraginops* Prado and *Paratraginops* Hendel); katepisternum with a dorsal row of two to four strong katepisternal bristles and some finer setulae; anepisternum bare (*Odinia* and *Traginops*) or bristled (*Neoalticomerus*); remaining pleural sclerites without bristles or setulae. Prosternum free, bare.

Wing (Fig. 3) rather short and broad, with well-developed anal angle and alula, variously patterned with brown spots, always darkened in vicinity of subcostal break in Nearctic species (not always so in exotic forms). C extending to M_1 (*Traginops*, Fig. 3) or ending at R_{4+5} (*Odinia* and *Neoalticomerus*), with subcostal break only, weakened but not broken in vicinity of costagial break; costal spines absent. Sc incomplete. Base of R bare; R_1 ending close to subcostal break and well before middle of wing; cells bm and dm present and separated by crossvein bm-cu; crossvein r-m joining M well beyond middle of cell dm; crossvein dm-cu usually present, obsolescent, or absent in *Neoalticomerus* (and several exotic genera). Cell cu*p* convexly closed. A_1 not attaining wing margin. Upper calypter moderately developed, whitish with concolorous margin and fringe; fringe uniform in length; lower calypter linear. Halter entirely whitish.

Legs (Fig. 1) rather short and stout, usually extensively yellowish. Fore femur with posterodorsal and posteroventral series of bristles; mid femur without strong bristles; hind femur enlarged in males, with one or more anteroventral bristles on apical half. Tibiae usually with alternating brownish and yellow bands; preapical dorsal tibial bristle weak to moderately strong, strongest on mid tibia; mid and hind tibiae with strong apicoventral bristles. Tarsi simple, mostly yellowish.

Abdomen: rather short and broad, usually grayish pruinose, patterned with contrasting brown pruinose spots.

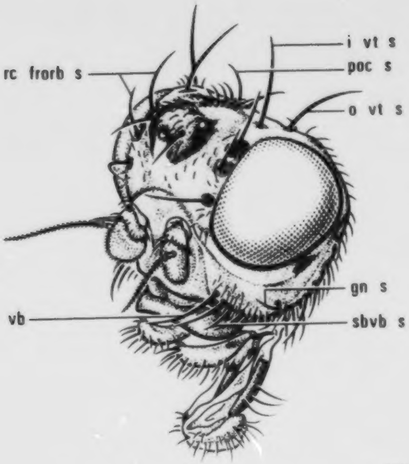
Male with six (*Odinia*) or seven spiracles (*Traginops*, Fig. 4). Sternite 5 relatively large and unmodified; sternites 6 and 7 greatly reduced and shifted into left side of abdomen, partially fused with each other and with remnants of segment 8. Tergite 6 reduced to narrow strip (*Odinia*) or absent (*Traginops*); tergite 7 relatively well-developed, bare; syntergosternite 8 larger than tergite 7, setulose posteriorly (*Traginops*) or bare (*Odinia*). Epandrium higher than long in lateral view, setulose, and sometimes with strong bristles (*Traginops*), with a surstylus-like posteroventral lobe arising either anterior to surstylus (*Traginops* and *Odinia*) (Fig. 4) or posterior to surstylus (*Neoalticomerus*). Surstylus large (*Traginops* and *Neoalticomerus*) or greatly reduced (*Odinia*), articulated, not fused, with lower margin of epandrium. Hypandrium (Fig. 5) with anterior margin projecting far forward; gonopod in form of a low shoulder-like lobe bearing specialized setulae; these setulae very long and wispy in *Traginops* (Fig. 5); parameres relatively free and process-like, densely setulose in *Traginops* but practically bare in *Odinia* and *Neoalticomerus;* aedeagus greatly reduced in *Neoalticomerus*, short and semimembranous in *Traginops* (Fig. 5), larger and longer in *Odinia* with rigid basal section and flimsy apical portion; a small epiphallus present in *Traginops*, absent in *Odinia* and *Neoalticomerus;* aedeagal apodeme unusually long, strongly sclerotized, rod-like; ejaculatory apodeme not evident. Cerci large and distinct in *Traginops* (Fig. 4), smaller and closely associated with epandrium in *Odinia* and *Neoalticomerus*.

Female with all segments beyond segment 5 modified (Fig. 6). Tergite 6 much smaller than previous tergites but otherwise normal; sternite 6 entire (*Odinia*) to more or less tripartite, with an elongate median and a shorter lateral plate on each side (*Traginops*); sixth spiracle in membrane between tergite 6 and sternite 6. Tergite 7 consisting of a bare relatively heavily sclerotized basal portion and a setulose but largely membranous apical portion; basal portion deeply emarginate (*Traginops*) to entirely divided dorsally (*Odinia*); sides extending laterally well onto ventral surface, and enclosing seventh spiracle in ventral margin; sternite 7 likewise with a very small bare relatively heavily sclerotized anterior plate and a setulose but membranous posterior part. Segment 8 tubular and membranous, with a few setulae on both dorsal and ventral surfaces near apex; cerci completely separate, rather long and slender with long hair-like setulae; epiproct and hypoproct distinct and plate-like, with a variety of hairs and setulae. Two sclerotized dome-like spermathecae usually present, but possibly three occurring in *Neoalticomerus* (Máca 1978).

Larva. Whitish, slender, subcylindrical, with 11 body segments and a small cephalic segment (Teskey 1976) (Fig. 7). Cephalopharyngeal skeleton for known species similar to that of other acalyptrate Muscomorpha, with hypopharyngeal and tentoropharyngeal sclerites separated, and with parastomal bars and simple mandibles present (Fig. 9). Anterior spiracle palmate, with 5–12 short papillae projecting marginally from expanded apex of spiracular stalk (Fig. 8). Ventral creeping welts with transverse rows of small spines present on abdominal segments 2–7 only; central spines on each welt larger than others. Posterior spiracles very small, situated on short outgrowths from one prominence or from a partially united pair of dome-shaped prominences on the terminal abdominal segment (Fig. 7).

Hennig (1938) provided good figures for *Odinia maculata* Meigen, and Shewell (1960) did likewise for *Traginops irrorata* Coquillett and *Neoalticomerus seamansi* Shewell.

Biology and behavior. The biology of the family was most recently and most precisely treated by Krivosheina (1979). Other important papers include those of Hennig (1938*a*, 1938*b*, 1965), Collin (1952), Sabrosky (1959), Shewell (1960), Zubkov and Kovalev (1975), Cogan (1975), and Teskey (1976). The larvae of most species whose biologies are known are associated with wounded, dead, or dying trees, where they are usually found in galleries of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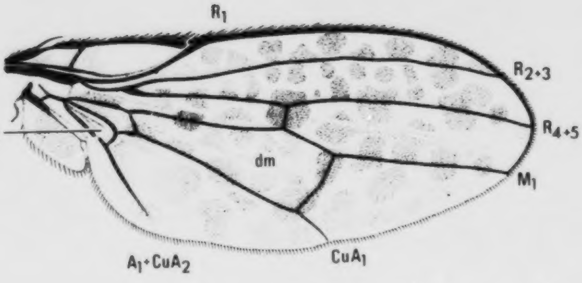
2 Traginops irrorata ♂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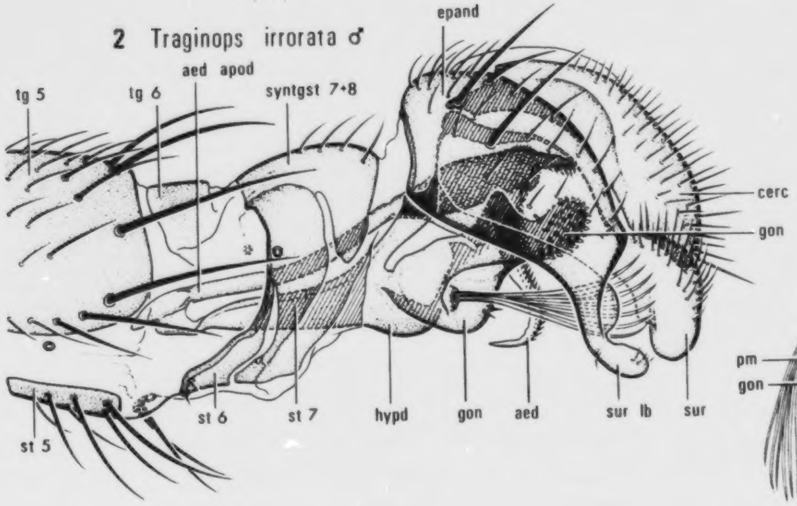
3 Traginops irrorata ♂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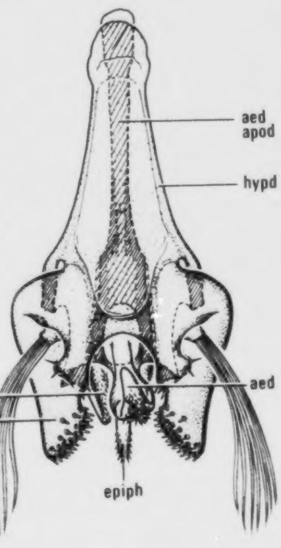
4 Traginops irrorata ♂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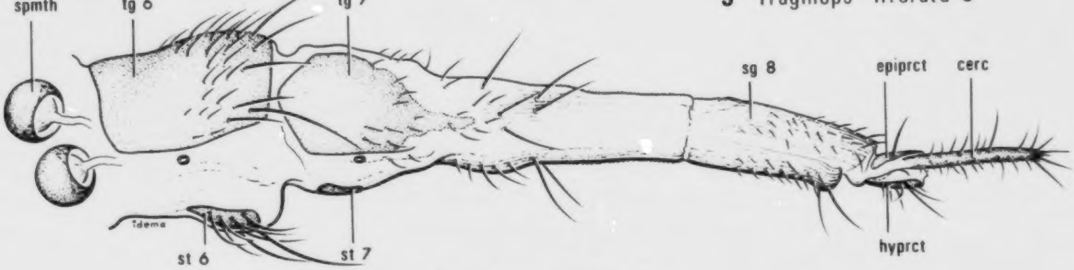
5 Traginops irrorata ♂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6 Traginops irrorata ♀

Figs. 72.2–6. Adult of *Traginops irrorata* Coquillett: (2) left anterolateral view of head; (3) dorsal view of right wing; (4) left lateral view of male terminalia; (5) ventral view of hypandrium and associated parts; (6) left lateral view of female terminalia.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gn s, genal seta; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; i vt s, inner vertical seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; rc frorb s, reclinate fronto-orbital seta; sg, segment; spmth, spermatheca; st, sternite; sbvb s, subvibrissal seta; sur, surstylus; sur lb, surstylar lobe; syntgst, syntergosternite; tg, tergite; vb, vibrissa.

wood-boring beetles and moths. Most authors are inclined to the view that the larvae are saprophagous. Cogan (1975) believed that they are probably mycophagous, feeding either on various fungi that develop in damaged trees or that grow in the galleries of original wood-boring insects. However, Krivosheina (1979) reported that several Palaearctic species are truly parasitic on larvae of other wood-infesting Diptera, i.e. *Hesperinus* sp. and *Pachyneura* sp.

Adults are most frequently taken on tree trunks, especially in the vicinity of fluxes or on fungi, or are reared from immature stages. A few have been collected in fruit-fly traps (Sabrosky 1959, Steyskal 1963).

Classification and distribution. The systematic position of the Odiniidae has been highly debated (see especially Frey 1921; Griffiths 1972; Hennig 1938*a*, 1938*b*, 1958, 1965, 1969, 1973). The family is now considered to be a generalized sister group of the Agromyzidae. The large exposed lunule in both sexes and the presence in the male of an unusually long, strong, aedeagal apodeme, combined with a peculiar, long, anteriorly narrowed hypandrium and other similarities (Spencer 1969), are accepted as valid synapomorphies. Other characters shared by both families, and also by most Clusiidae, are inwardly directed frontal bristles, the presence of a subcostal break, a shortened anal vein, and two spermathecae. Two important autapomorphic characters of the Odiniidae are the absence of a sclerotized ejaculatory apodeme and a secondarily reduced, simple aedeagus.

The family is represented on all the main continents, and 10 extant genera are now recognized (Shewell 1960, Hennig 1969, Prado 1973, Cogan 1975, Krivosheina 1979), as follows: *Afrodinia* Cogan (Ethiopian), *Lopesiodinia* Prado (Neotropical), *Neoalticomerus* (Holarctic), *Neotraginops* (Neotropical), *Odinia* (Holarctic, Neotropical, Ethiopian, Oriental, and Australian), *Paratraginops* (Neotropical), *Schildomyia* Malloch (Neotropical and Oriental), *Shewellia* Hennig (Neotropical), *Traginops* (Nearctic, Neotropical, Ethiopian, Oriental, and Australian), and *Turanodinia* Stackelberg (Palaearctic, Ethiopian, and Oriental). Hennig (1965) divided the family into two subfamilies, the Odiniinae (*Afrodinia*, *Odinia*, *Neoalticomerus*, and *Turanodinia*) and the Traginopinae (*Lopesiodinia*, *Neotraginops*, *Paratraginops*, *Schildomyia*, *Shewellia*, and *Traginops*). Altogether, about 50 species are known in the world, but only about 12 species, eight of which are in *Odinia*, one in *Neoalticomerus*, and two in *Traginops*, are known from the Nearctic region.

One fossil species, *Protodinia electrica* Hennig from Baltic amber, is known (Hennig 1965). In that species the ocellar plate does not protrude, the disc of the scutellum is bare, and C appears to end at R_{4+5}. All these characters indicate it belongs to the subfamily Odiniinae.

Key to genera

1. Disc of scutellum setulose. Ocellar plate unusually prominent (Fig. 2). C extending to M_1 (Fig. 3) .... TRAGINOPINAE.... ***Traginops*** Coquillett

   2 spp.; southeastern to midwestern; Steyskal 1963

   Disc of scutellum bare. Ocellar plate normal (Fig. 1). C extending only as far as R_{4+5} ... . ODINIINAE....2

2. Anepisternum with bristles; scutum with one to three dorsocentral bristles .... ***Neoalticomerus*** Hendel

   1 sp., *seamansi* Shewell; Alberta, Arizona, Nebraska, New Brunswick; Shewell 1960

   Anepisternum bare; scutum with one to four dorsocentral bristles (Fig. 1) .... ***Odinia*** Robineau-Desvoidy

   8 spp.; Sabrosky 1959

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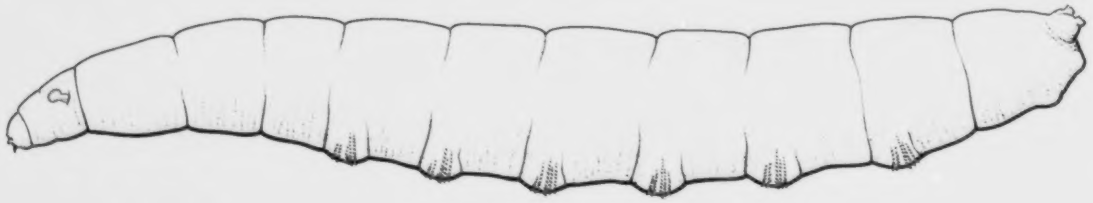
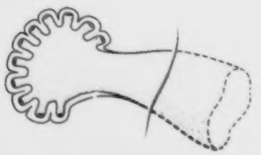
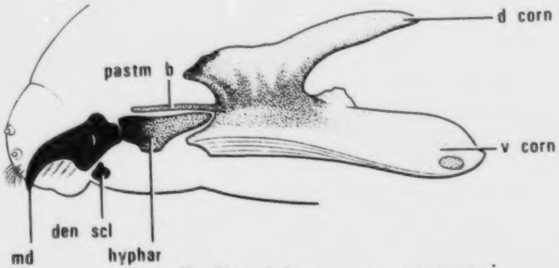


7 Neoalticomerus seamansi



8 Neoalticomerus seamansi



9 Neoalticomerus seamansi

Figs. 72.7-9. Larva of *Neoalticomerus seamansi* Shewell: (7) left lateral view of mature larva; (8) details of anterior spiracle; (9) details of cephalopharyngeal skeleton.

Abbreviations: d corn, dorsal cornu; den scl, dental sclerite; hyphar, hypopharynx; md, mandible; pastm b, parastomal bar.

AGROMYZIDAE

73

K. A. SPENCER

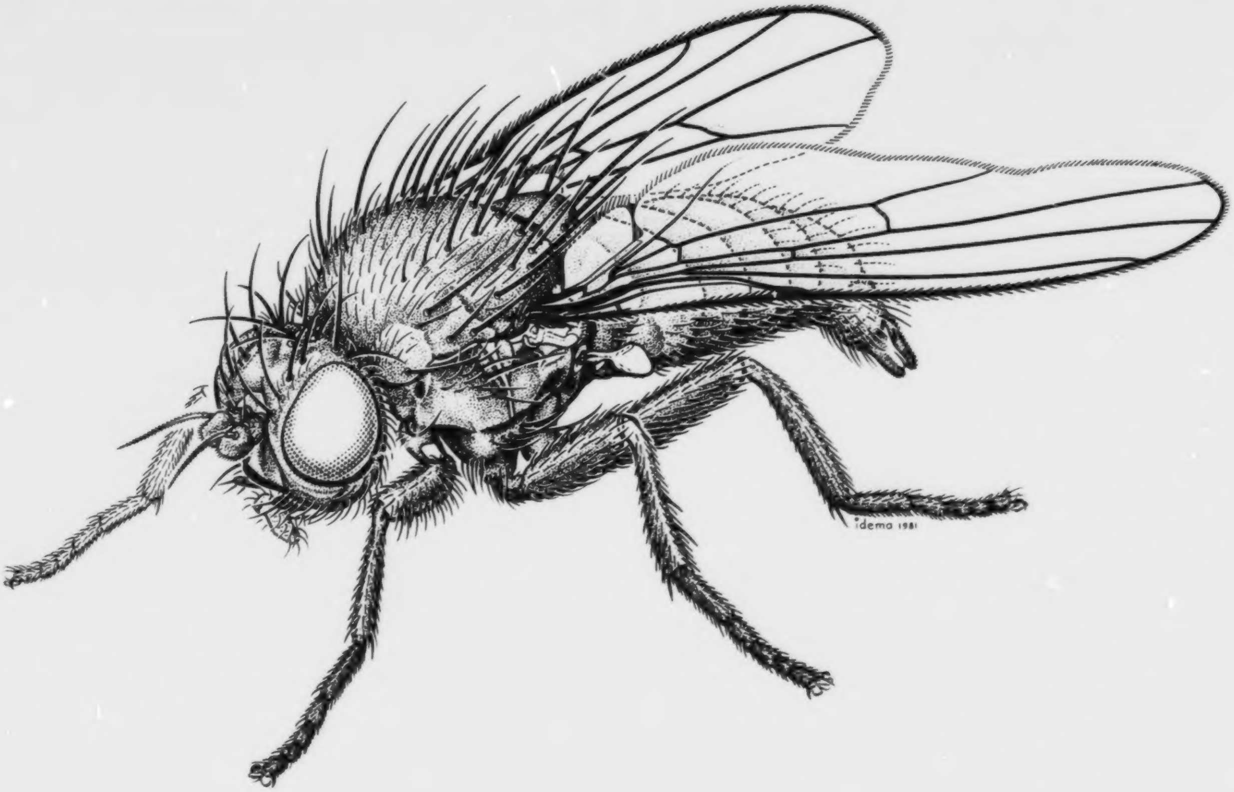


Fig. 73.1. Female of *Agromyza albipennis* Meigen.

Minute to medium-sized flies (Fig. 1), with wing length 0.9–6.5 mm. Postocellar bristles when present divergent, absent in *Xeniomyza* Hering and *Penetagromyza* Spencer. Color ranging from black, gray, or green to entirely yellow; wing normally hyaline, but in a few tropical species of the Old and New Worlds distinctively pictured or infuscated.

Adult. Head (Figs. 2–8): eye upright or conspicuously slanting, bare or pilose (frequently only in male). Ocellar triangle inconspicuous to brilliantly shining, normally black, sometimes gray or greenish, short or extending to margin of lunule, and of varying width. Frons from three times wider than eye to less than width of eye; frontal vitta normally bare, but rarely with a few scattered setulae near lunule; fronto-orbital plate frequently little differentiated from frons, sometimes broad and raised, with from one to three orbital bristles and one to five frontal bristles, and with a variable number of fronto-orbital setulae occurring in one or more rows near eye margin; these either proclinate (Fig. 3) or upright or reclinate (Figs. 2, 7, 8). Face weakly concave or with conspicuously raised carina, particularly in *Ophiomyia* (Fig. 4). Gena varying from linear to half height of eye, with a well-developed vibrissa (Figs. 2, 3) or with a bunch of fused (fasciculate) vibrissae in male of many species of *Ophiomyia* Braschnikov (Fig. 4); clypeus usually relatively large and exposed; frontoclypeal membrane sometimes large and conspicuous. Proboscis normally short, sometimes conspicuously elongate; palpus small, normally slender. First flagellomere varying from small and round to elongate, bare or distinctly pilose; arista short and bare, or longer and more pubescent.

Thorax: mesonotum longer than broad (Fig. 1), approximately rectangular; transverse suture visible only on lateral margins. Postpronotal lobe well-developed. Chaetotaxy: two dorsocentral bristles normally present in *Melanagromyza* Hendel, *Ophiomyia*, and *Japanagromyza* Sasakawa; up to five postsutural bristles in some species of *Agromyza* Fallén or three postsutural and one presutural in other *Agromyza* spp. and in all Phytomyzinae; one pair of prescutellar acrostichal bristles present or lacking; acrostichal setulae varying from numerous, in up to 10 rows, to entirely lacking; one postpronotal bristle, two (rarely one) notopleural bristles, one anepisternal bristle, and one katepisternal bristle present; intra-alar, supra-alar, and postalar bristles present or lacking; proepisternal bristle normally present, absent only in *Gymnophytomyza* Hendel (Palaearctic); two pairs of scutellar bristles usually present, but only one in subgenera *Cerodontha* Rondani and *Xenophytomyza* Frey of *Cerodontha*. Legs slender, with two or more anterolateral bristles sometimes present on mid tibia, and with one sometimes present on fore tibia in *Melanagromyza* and *Japanagromyza*, but always present in *Nemorimyza* Frey; preapical dorsal tibial bristle usually absent on all tibiae. Wing (Figs. 9–12) normally hyaline, rarely darkened, brownish or infuscated in subcostal area, conspicuously pictured in some species of *Phytobia* Lioy (Neotropical); C extending to apex of M_{1+2} or ending near R_{4+5}, broken only at apex of Sc; Sc either distinct and joining R_1 (Agromyzinae, Fig. 9) or reduced to a fold that remains free from R_1, but which may or may not reach C (Phytomyzinae, Figs. 10–12); R_1 bare; crossvein r-m present; crossvein dm-cu present or absent; cell cu*p* present; A_1 not reaching wing margin.

Abdomen: normally conspicuously tapering (Fig. 1), more rarely narrow and elongate, composed of six visible segments and terminalia. Seven spiracles usually present in both sexes. Stridulating mechanism present in both sexes in *Agromyza* and in male of *Liriomyza* Mik (von Tschirnhaus 1971), consisting of a scraper, a sclerotized ridge on inner surface of hind femur (Fig. 14), and a file of sclerotized scales on connecting membrane below anterior tergites (Fig. 13).

Female terminalia (Figs. 21, 22) consisting of highly modified segments 7–9. Segment 7 visible externally as a conical nonretractile oviscape, either shining black or variably pubescent, and sometimes greatly elongated as in *Phytomyza varipes* Macquart (Fig. 21); anterior part telescoped into preceding segment. Eversible ovipositor sheath, i.e. posterior part of segment 7 and intersegmental membrane between segments 7 and 8, bearing anteriorly directed denticles of varying size and shape; denticles used for boring into plant tissue for oviposition. Segment 8, ventrally, with a pair of egg guides of varying size and shape bearing various sensory processes on hind margin. Proctiger variously modified, with epiproct normally larger than hypoproct, and carrying short separate cerci on hind margin. Two sclerotized spermathecae present. A detailed description of female terminalia and internal reproductive system given by Sasakawa (1958) and Ipe (1966).

Male terminalia with sternites 6 and 7 lost, and with segment 8 reduced to a narrow inverted band lying dorsally behind remnants of segments 6 and 7. Epandrium with a distinctive arrangement of bristles, particularly in *Melanagromyza* and *Phytoliriomyza* Hendel (Fig. 15). Surstylus fused with lower corner of epandrium in Agromyzinae, but fused (*Phytomyza* Fallén) or discrete (*Phytobia*, *Liriomyza*) in Phytomyzinae. Hypandrium U-shaped, open posteriorly; gonopods reduced, fused with hypandrium; parameres relatively strongly developed; aedeagus (Figs. 18–20) greatly varying in shape, with considerable sclerotization in all genera except *Haplomyza* Hendel; basal sclerites asymmetric and articulated to the cylindrical aedeagal apodeme; distal section consisting of a distiphallus with two gonopores in what is frequently seen as symmetric sclerotized tubules (Fig. 15) or one gonopore in a single tubule; aedeagus at rest lying within genital pouch with distiphallus anterior to basiphallus, but for copulation aedeagus swings back through 180°; a strong rod-like aedeagal apodeme present internally above aedeagus, extending far into abdomen (Figs. 15, 16) (Nowakowski 1962, Griffiths 1972*a*); ejaculatory apodeme (Figs. 15, 16) varying in size and shape, but typically fan-shaped, sometimes with a conspicuous bowl-shaped base (*Amauromyza* Hendel and some species of *Liriomyza*).

Egg. Oval or slightly reniform, white or yellowish, with micropyle at the slightly blunter end.

Larva. Cylindrical, slightly tapering at front and rear, with normal cephalic segment, three thoracic segments, and eight detectable abdominal segments (Fig. 24). Most species 1.5–3 mm long, but in *Phytobia* body unusually extended while feeding in internal channels in trees, sometimes attaining a length of 25 mm.

Strongly sclerotized mandibles paired, linked slightly asymmetrically but moving as a single unit, and each consisting of two or more teeth of variable size and shape (Figs. 23, 27). Several sensory organs lying above mandibles, including short antennae, rudimentary maxillary palpi, and minute labial papilli. A fairly long finger-like frontal projection (Stirnfortsatz) present in some *Phytomyza* spp. A short sclerotized hypopharyngeal sclerite present, linking mandibles to a biramous tentoropharyngeal sclerite; the dorsal and sometimes ventral cornua of tentoropharyngeal sclerite with prominent clear windows that appear to divide the upper cornu into two arms in Agromyzinae (Fig. 27), but these clear windows absent in upper cornu in Phytomyzinae (Fig. 23).

Anterior spiracles situated dorsal to frontal projection, and varying greatly in shape and in number of actual spiracular openings (bulbs); plesiomorphic state consisting of five openings, but the highly apomorphic Palaearctic species *Agromyza alunulata* Hendel with up to 250 openings; each ellipse or grouping of openings borne on a low projection (Figs. 25, 29, 31), but in some species spiracles substantially longer and even asymmetric. Posterior spiracles frequently important taxonomically; plesiomorphic condition with three openings retained in many species such as in *Agromyza*, *Liriomyza*, and *Phytobia* (Fig. 28); *Melanagromyza* with an ellipse of openings varying from 5 to 20 surrounding a distinctive central horn (Fig. 30), although horn is reduced to a vestigial scar in a few species; some species of *Liriomyza* with up to 10 spiracular openings, one sometimes extended (Fig. 32); *Phytomyza* having the most openings, usually with 20 or more (Fig. 26).

A varied arrangement of cuticular processes lying around each segment near the front margin; processes strongest on dorsal surface, and sometimes of specific significance.

Puparium. Shape, form, and color varying greatly with genera and species. Form of larval spiracles retained in puparium, although detail not always as clear. Puparium barrel-shaped, with or without segmentation, or conspicuously elongate (*Napomyza* Westwood); surface smooth, shining, indented with fine lateral lines (nadelrissig of Hering), or roughened with cuticular processes present in larva. Color varying from deep black through orange brown to yellowish white.

Biology and behavior. Larvae of all Agromyzidae feed on living plant tissue, and the few records suggesting otherwise can only be the result of inaccurate observation. The egg is laid beneath the epidermis of the plant at the appropriate oviposition site. The young larva normally emerges within a few days; while feeding, it forms a channel or mine within the plant, which in most cases is entirely species-specific. The larva feeds from about 1 week to several months. The temperature can cause minor variations in the feeding period, but the duration of this stage is essentially fundamental to the life cycle. Species that have several generations a year in quick succession feed rapidly, whereas those with only a single generation a year feed more slowly and in some cases intermittently throughout the colder winter months.

Pupation normally takes place on the ground; the larva either falls from the plant to the ground where it transforms after a few hours, or it transforms immediately on leaving the leaf and falls to the ground as a puparium. A few leaf miners pupate within the leaf at the end of a mine, and most seed feeders and stem borers pupate within the plant at the feeding site. Pupation lasts from 5 days to as long as 6–10 months, depending on the species.

The Agromyzidae are known best as leaf miners. However, they attack all parts of the plant, including stems, seeds, and roots, and the young trunks and twigs of trees.

The form of the leaf mine is a substantial aid in identifying Agromyzidae species. Although individual mines can vary considerably, the pattern essentially remains constant for each species. Mines are basically linear, serpentine (Fig. 33), or blotch-like; blotch-like mines are approximately circular, elongate (Fig. 34), or irregular in shape with short offshoots (Fig. 35). The short, linear mine often formed by the larva in the first instar sometimes changes after the first molt to a blotch-like mine, which can completely envelop the earlier linear section. The part of the leaf that is mined is also frequently significant. Most mines are formed on the upper surface of the leaf, within the palisade parenchyma; more rarely, shallow mines are made immediately beneath the epidermis of the leaf, as by *Liriomyza schmidti* (Aldrich), or exclusively on the lower surface of the leaf in the spongy parenchyma. Some mines are invariably associated with the margin of the leaf; others occur exclusively along the midrib or possibly along one of the stronger lateral veins. The arrangement of frass in the mine is often characteristic; it is sometimes deposited in single, widely spaced pellets, or in more-or-less continuous strips, or in one mass immediately before pupation at the end of the mine and to which the puparium is sometimes firmly glued.

Most Agromyzidae are either monophagous, limiting their choice of host to a single species of plant or to several species within the same genus, or oligophagous, feeding on several genera within a single family or on several related families of the same order. Few species are truly polyphagous, feeding on a wide range of unrelated hosts. Common polyphagous species in North America are *Liriomyza huidobrensis* (Blanchard) and *L. sativae* Blanchard.

The worldwide economic importance of the Agromyzidae was recently discussed by Spencer (1973). Damage can be caused to trees by larvae boring in the growing wood (*Phytobia*), to beans and other leguminous plants by species feeding in stems and pods (*Melanagromyza, Ophiomyia*), and to many plants by leaf miners (*Agromyza, Liriomyza, Phytomyza*). Some 150 species of crop plants suffer some damage, but several of the most serious pests, such as *Ophiomyia phaseoli* (Tryon) on beans, are mainly limited to the Tropics of the Old World.

In North America the most serious damage is caused by leaf miners in the genus *Liriomyza*, particularly in Florida and California. The three species *L. huidobrensis*, *L. sativae*, and *L. trifolii* (Burgess) are all highly polyphagous, and among their hosts the plants most frequently attacked are tomatoes, cucumbers, squash, beans, and celery, and among ornamentals aster, chrysanthemum, and gypsophila.

Classification and distribution. The family Agromyzidae is so highly differentiated from all possibly related families that it has been constantly rearranged in systems of higher classification by leading dipterists such as Hendel, Malloch, Frey, and Hennig. Frick (1952) reviewed the various changes proposed up to then in the systematic position of the family. Hennig (1958) included the Agromyzidae among families of uncertain relationship but considered it most closely related to the Odiniidae (or possibly the Clusiidae), and in 1973 he united the Agromyzidae and Odiniidae in the superfamily Agromyzoidea.

In the most detailed comparative study of the male terminalia of the Muscomorpha yet undertaken, Griffiths (1972*a*) concluded that the family Agromyzidae was a sister group of the Clusiidae and placed the two in the prefamily Agromyzoinea.

The Agromyzidae are characterized as a monophyletic group by the following combination of characters (Hennig 1958): vibrissae present (Figs. 1–4); one to seven frontal bristles present (Figs. 1–5); costal break present at the apex of Sc; cell cu*p* small; A_1 not reaching wing margin (Figs. 9–12); pregenital sclerites of male with a simple (fused) tergal complex (tergites 6–8) with only two spiracles between tergite 5 and the genital segment; and anterior part of abdominal segment 7 in female forming an oviscape.

The division of the Agromyzidae into the two subfamilies Agromyzinae and Phytomyzinae is based on the differing course of Sc and the different structure of the larval cephalopharyngeal skeleton. This treatment was proposed by Hendel (1931) and has been followed in all subsequent comprehensive systematic works on the family. Von Tschirnhaus (1971) reexamined these characters and correctly pointed out that there is, in fact, no rigid distinction between the two subfamilies. In *Phytobia* (Phytomyzinae), for example, Sc frequently appears as in the Agromyzinae; and in a few isolated cases in the Phytomyzinae, a vestigial lower area of the larval cephalopharyngeal skeleton is evident, approaching the condition of the Agromyzinae. These exceptions do not themselves disprove the monophyletic origin of the two subfamilies, and even with the fairly small number of genera described in the family, this subfamilial division remains of practical value.

Only 27 genera are considered valid in the Agromyzidae at present, and of these, 19 are known in the Nearctic region. The list of world genera given by Spencer (1969) has been revised since then. In the Agromyzinae, *Geratomyza* Spencer (Spencer and Stegmaier 1973) was erected as a small Neotropical segregate of *Agromyza*, and *Tropicomyia* Spencer (1973) was erected for the widespread group of epidermal leaf miners extending throughout the Tropics of the Old World to northern Australia. *Trilobomyza* Hendel, *Melanophytobia* Hering, and *Campanulomyza* Nowakowski are now included in *Amauromyza*, and *Catalpomyza* Spencer has recently been erected as a further subgenus in *Amauromyza* (Spencer 1977). *Praspedomyza* Hendel is now treated as synonymous with *Liriomyza*. *Lemurimyza* Spencer, *Pteridomyza* Nowakowski, and *Nesomyza* Spencer have now been synonymized with *Phytoliriomyza* (cf. Spencer 1974). Griffiths (1974*a*) has resurrected *Chromatomyia* Hardy.

Frick (1959) produced an important synoptic revision of North American species, but this work was substantially revised by Spencer (1969) and Spencer and Stegmaier (1973). Five new American *Phytomyza* species were described by Kulp (1968), 21 species in six genera were described from Alberta by Sehgal (1971), and five new American species were described by Steyskal (1972) from Michigan. Griffiths (1972*b*, 1972*c*, 1973*a*, 1973*b*, 1974*a*, 1974*b*, 1974*c*, 1974*d*, 1975, 1976*a*, 1976*b*, 1976*c*) has described 37 new species from Alaska and western Canada and has recorded 20 Palaearctic species as new to the Nearctic region in a continuing series of papers on boreal species. Spencer (1977) described one new American *Agromyza* species.

Over 2500 species of Agromyzidae are known in 27 genera, but the total world fauna probably exceeds 3500 species. The family is distributed throughout the world, and habitats range from Arctic tundra to the Tropics.

The greatest proliferation of species occurs in temperate areas of the Northern Hemisphere, where approximately 70% are found. The Holarctic region has about 45% of the known species, but the Nearctic region has only 25%. Little specialized collecting has been undertaken in North America and hundreds of species probably remain to be described, particularly in the mountain ranges of the United States.

The distribution of the main genera varies significantly between temperate and tropical areas. *Phytomyza*, the largest genus with 400 species, is dominant in the Palaearctic and Nearctic regions but is reduced to only a few species in the Tropics and the Southern Hemisphere. *Liriomyza*, which is the third largest world genus with 250 species, is similarly reduced in the Ethiopian, Oriental, and Australian regions but is better represented in the Neotropical region. The dominant genus in the Tropics is *Melanagromyza*, with about 300 species.

Several fossil Agromyzidae have been described, but Hennig (1965) concluded that all such records were doubtful and that no Agromyzidae fossils are known from amber. Recently, however, *Palaeophytobia platani* Süss & Müller-Stoll has been described from the characteristic feeding channels of the larva in Upper Miocene wood fragments of *Platanoxylon hungaricum*, a plane tree from Hungary (Süss and Müller-Stoll 1975). The modern genus, *Phytobia*, is one of the most primitive in the family.

Key to genera

1. Sc developed throughout its length (Fig. 9), coalescing with R_1 before reaching C; R_1 expanded at junction with C, its caudal margin sinuous near junction; deep notch in C at subcostal break . . . . AGROMYZINAE 2

Sc incomplete distally or merely a fold (Figs. 10–12), ending in C separately and basally of R_1; R_1 at most only slightly expanded at junction with C, its caudal margin straight or slightly concave approaching C; costal margin only slightly if at all notched at subcostal break . . . . PHYTOMYZINAE 6

2. At least three pairs of dorsocentral bristles and a prescutellar acrostichal bristle always present; halter white or yellow; presutural dorsocentral bristle frequently present (Fig. 1); stridulating mechanism present in both sexes (Figs. 13, 14) . . . . ***Agromyza*** Fallén

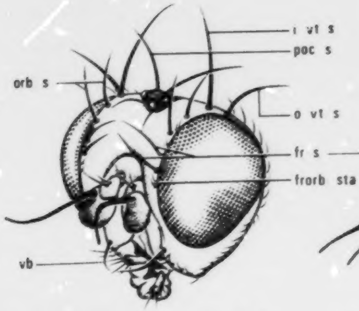
42 spp.; Canada to Mexico; Spencer 1969, Sehgal 1971

Two pairs of dorsocentral bristles usually present; if three or four pairs present, halter black; presutural dorsocentral bristle rarely present; no stridulating mechanism present 3

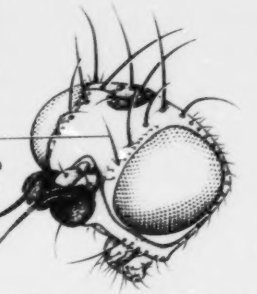
3. Either prescutellar acrostichal or fore tibial bristle present, or halter yellowish . . . . ***Japanagromyza*** Sasakawa

7 spp.; eastern U.S.A. to Florida; Spencer and Stegmaier 1973

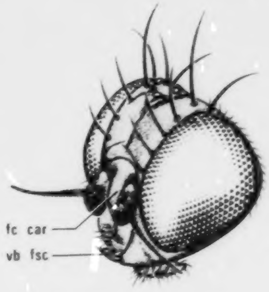
Prescutellar acrostichal bristle absent; halter usually black (white in *Ophiomyia aberrans* Spencer, South Africa) 4


i vt s
poc s
orb s
o vt s
fr s
frorb sta
vb

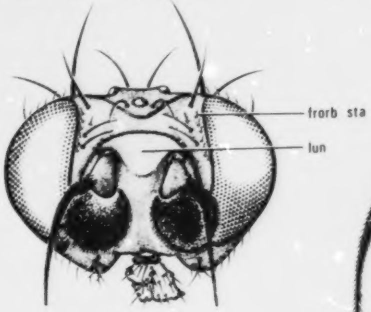
2 Liriomyza septentrionalis ♀



3 Phytomyza pedicularidis ♀


fc car
vb fsc

4 Ophiomyia maura ♂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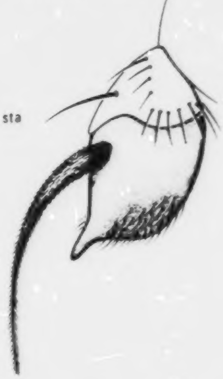
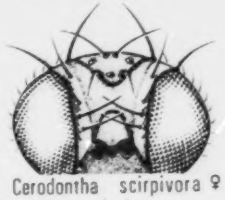
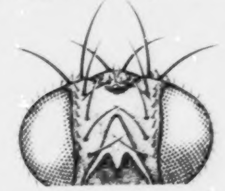
5 Cerodontha luctuosa ♂



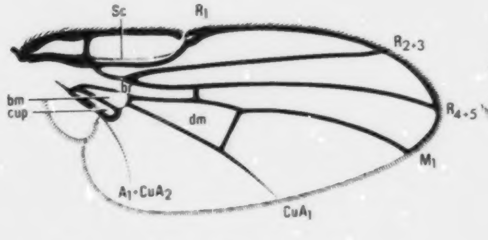
6 Cerodontha dorsalis ♀



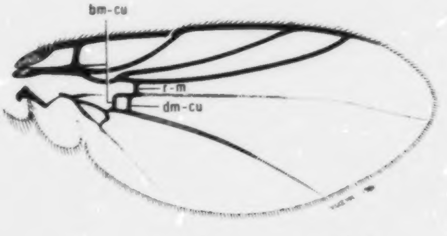
7 Cerodontha scirpivora ♀



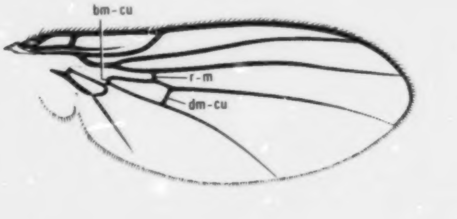
8 Cerodontha pygmaea ♀


Sc
R1
R2+3
bm
cup
br
dm
R4+5
M1
A1+CuA2
CuA1

9 Melanagromyza laetifica ♀


bm-cu
r-m
dm-cu

10 Napomyza lateralis ♀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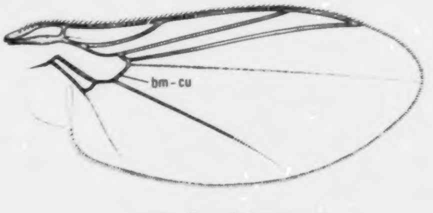
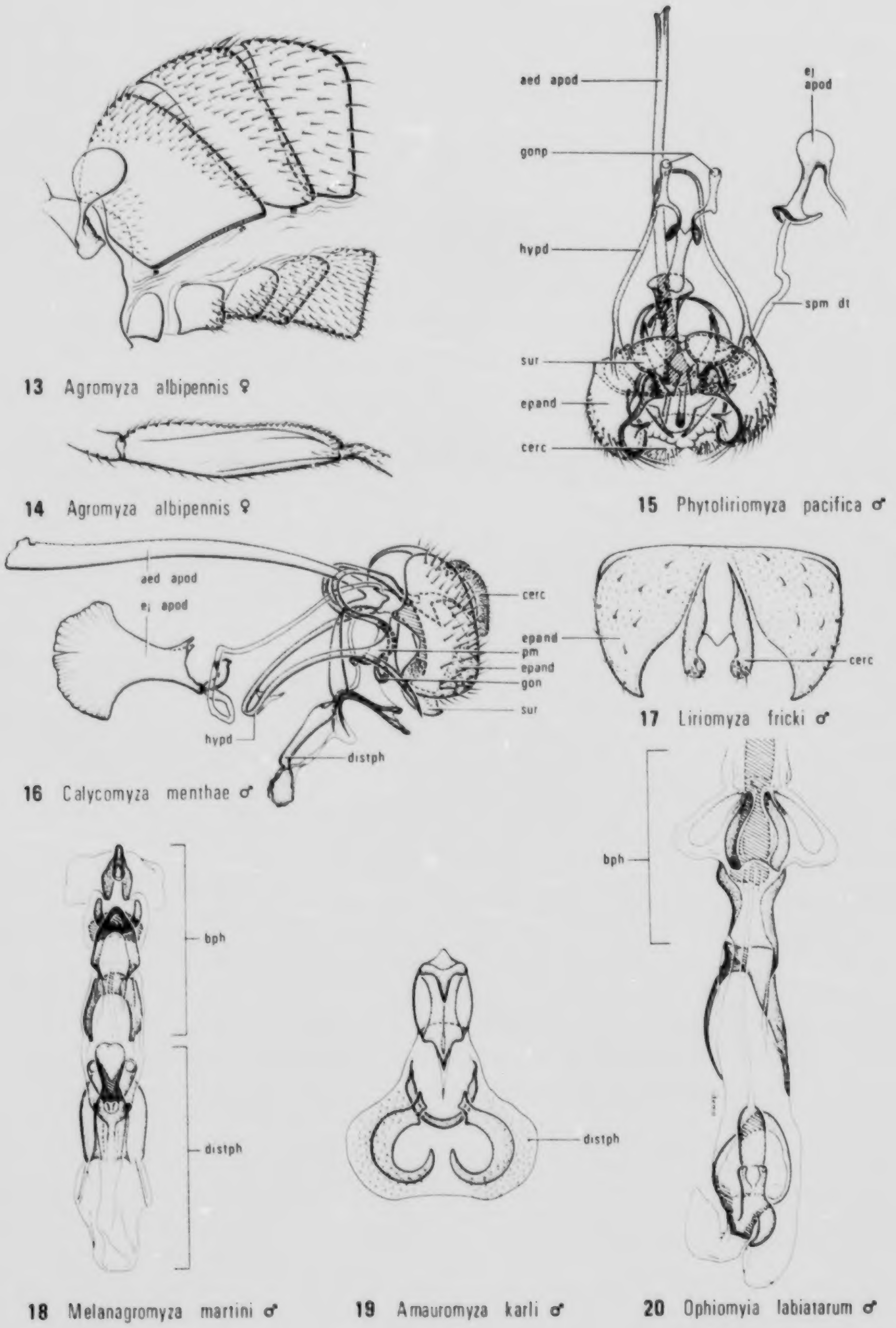
11 Paraphytomyza nitida ♀



12 Pseudonapomyza lacteipennis ♀

Figs. 73.2–12. Heads, antenna, and wings: oblique views of head of (2) *Liriomyza septentrionalis* Sehgal, (3) *Phytomyza pedicularidis* Spencer, and (4) *Ophiomyia maura* (Meigen); (5) anterior view of head of *Cerodontha luctuosa* (Meigen); (6) antenna of *Cerodontha dorsalis* (Loew); anterior views of head of (7) *Cerodontha scirpivora* Spencer and (8) *Cerodontha pygmaea* (Meigen); wings of (9) *Melanagromyza laetifica* Spencer, (10) *Napomyza lateralis* (Fallén), (11) *Paraphytomyza nitida* (Malloch), and (12) *Pseudonapomyza lacteipennis* (Malloch).

Abbreviations: fc car, facial carina; frorb sta, fronto-orbital setula; fr s, frontal bristle; i vt s, inner vertical bristle; lun, lunule; orb s, orbital bristle; o vt s, outer vertical bristle; poc s, postocellar bristle; vb, vibrissa; vb fsc, vibrissal fasciculus.



13 Agromyza albipennis ♀

14 Agromyza albipennis ♀

15 Phytoliriomyza pacifica ♂

16 Calycomyza menthae ♂

17 Liriomyza fricki ♂

18 Melanagromyza martini ♂

19 Amauromyza karli ♂

20 Ophiomyia labiatarum ♂

Figs. 73.13–20. Stridulatory mechanism and features of male terminalia: stridulatory structures of (13) first abdominal tergite and (14) hind femur of *Agromyza albipennis* Meigen; male terminalia of (15) *Phytoliriomyza pacifica* (Melander), ventral view, and (16) *Calycomyza menthae* Spencer, lateral view; (17) epandrium of *Liriomyza fricki* Spencer, posterior view; aedeagus of (18) *Melanagromyza martini* Spencer, (19) *Amauromyza karli* Hendel, and (20) *Ophiomyia labiatarum* Hering.

Abbreviations: aed apod, aedeagal apodeme; bph, basiphallus; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; gonp, gonopore; hypd, hypandrium; pm, paramere; spm dt, sperm duct; sur, surstylus.

4. Mesonotum or abdomen frequently with some greenish, bluish, or coppery metallic coloration. C extending strongly to M_{1+2} (Fig. 9). Aedeagus symmetric, with basiphallus U-shaped (Fig. 18). Larva an internal stem borer or seed feeder .... ***Melanagromyza*** Hendel
   56 spp.; Alaska to Mexico; Spencer 1969, Sehgal 1971, Spencer and Stegmaier 1973

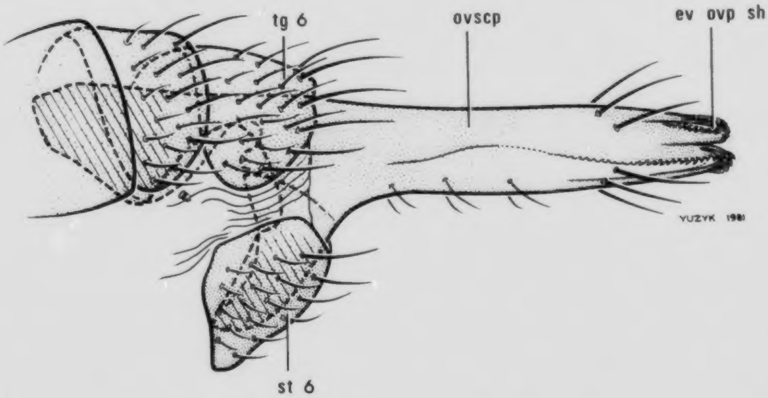
   Uniformly black species. C ending at R_{4+5} or continuing to M_{1+2}. Aedeagus frequently asymmetric, with basiphallus having conspicuously diverging side arms (Fig. 20). Habitats of larva variable 5

5. Antennae normally separated by conspicuous facial carina. Male frequently with distinct vibrissal fasciculus (Fig. 4) or with close grouping of smaller bristles around vibrissa. Larva a stem or leaf miner.. ***Ophiomyia*** Braschnikov
   35 spp.; Canada to Mexico; Spencer 1969, Spencer and Stegmaier 1973

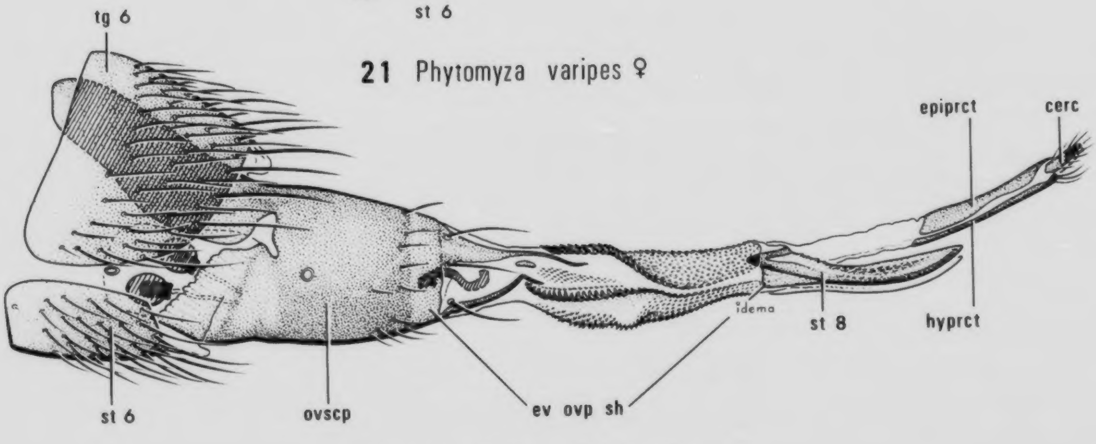
   Antennae closely adjoining each other. Vibrissal fasciculus or its precursor never present. Larva a gall causer .... ***Hexomyza*** Enderlein
   4 spp.; Canada, northern U.S.A.; Spencer 1969

6. Fronto-orbital setulae usually erect or reclinate, or absent (Figs. 2, 5, 7, 8) 7

   Fronto-orbital setulae distinctly proclinate (Fig. 3).. 22



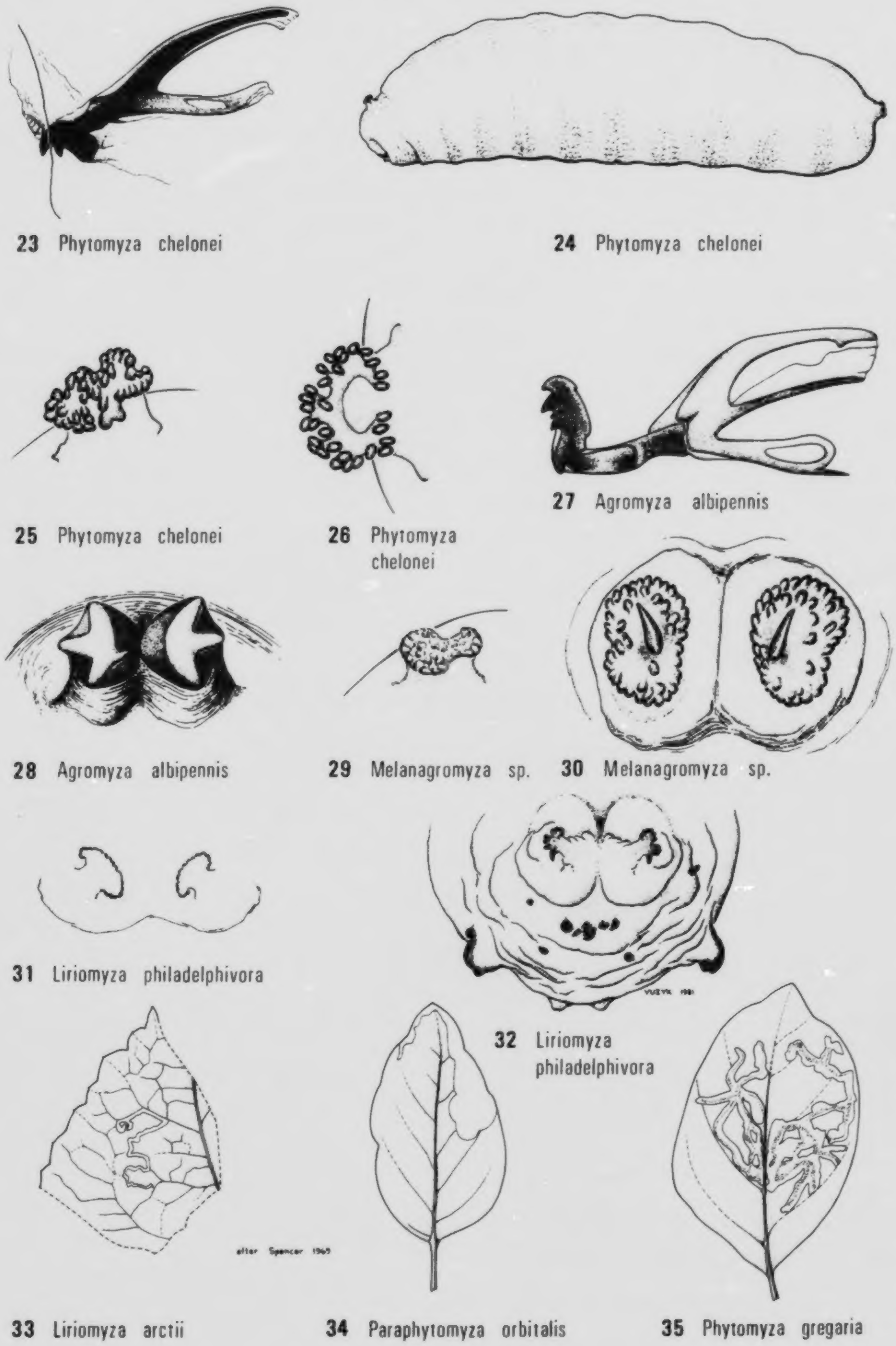
21 Phytomyza varipes ♀



22 Agromyza pseudoreptans ♀

Figs. 73.21–22. Female terminalia: (21) *Phytomyza varipes* Macquart, lateral view; (22) *Agromyza pseudoreptans* Nowakowski, ventral view.

Abbreviations: cerc, cercus; epiprct, epiproct; ev ovp sh, eversible ovipositor sheath; hyprct, hypoproct; ovscp, oviscape; st, sternite; sg, segment; tg, tergite.



23 Phytomyza chelonei

24 Phytomyza chelonei

25 Phytomyza chelonei

26 Phytomyza chelonei

27 Agromyza albipennis

28 Agromyza albipennis

29 Melanagromyza sp.

30 Melanagromyza sp.

31 Liriomyza philadelphivora

32 Liriomyza philadelphivora

33 Liriomyza arctii

34 Paraphytomyza orbitalis

35 Phytomyza gregaria

Figs. 73.23–35. Features of larvae and leaf mines: (23) cephalopharyngeal skeleton of *Phytomyza chelonei* Spencer; (24) larva of *P. chelonei*, lateral view; (25) anterior spiracle and (26) posterior spiracle of *P. chelonei*; (27) cephalopharyngeal skeleton and (28) posterior spiracle of *Agromyza albipennis* Meigen; (29) anterior spiracle and (30) posterior spiracles of *Melanagromyza* sp.; (31) anterior spiracles and (32) posterior view of abdomen of *Liriomyza philadelphivora* Spencer; leaf mines of (33) *Liriomyza arctii* Spencer, (34) *Paraphytomyza orbitalis* (Melander), and (35) *Phytomyza gregaria* Frick (after Kenneth A. Spencer 1969).

7. Wing with C extending to apex of M_{1+2}; if extending only to R_{4+5}, then either crossvein dm-cu absent, notopleural area black, species large, wing length 3 mm (*Phytobia coylesi* Spencer), or lunule substantially higher than semicircle (*Cerodontha flavocingulata* Hendel and *C. frankensis* Spencer) 8

C extending only to R_{4+5}; crossvein dm-cu absent 21

8. Scutellum normally dark, concolorous with mesonotum. If scutellum yellow, R_{4+5} ending nearer wing tip than does M_{1+2} 9

Scutellum yellow. M_{1+2} ending nearer wing tip than does R_{4+5} 18

9. Halter with knob white or yellow 10

Halter usually with knob black or at least partially darkened. If knob yellow (subgenus *Cephalomyza*), distiphallus with numerous spinules .... ***Amauromyza*** Hendel, in part

11 spp.; Canada to Mexico; Spencer 1969, Sehgal 1971

10. R_{4+5} ending nearer wing tip than does M_{1+2}. Scutellum yellow in *kallima* group (Neotropical) .... ***Phytobia*** Lioy

12 spp.; Canada to Mexico; Spencer 1969, Spencer and Stegmaier 1973

M_{1+2} ending nearer wing tip than does R_{4+5}. Scutellum black or yellow 11

11. First flagellomere with an apical spine (Fig. 6), and scutellum with only one pair of bristles; or lunule conspicuously higher than a semicircle, either narrow (Fig. 7) or triangular (Fig. 8); or lunule conspicuously large and broad (Fig. 5), antennal bases widely separated, and first flagellomere in male normally greatly enlarged (Fig. 5) .... ***Cerodontha*** Rondani

42 spp.; Alaska to Mexico; Spencer 1969, Spencer and Stegmaier 1973

Not agreeing with any of above combinations 12

12. Fore tibia with lateral bristle. Abdomen in male conspicuously yellow .... ***Nemorimyza*** Frey

1 sp., *posticata* Meigen; Canada to Florida, Mexico; Spencer 1969

Fore tibia never with lateral bristle; only mid tibia sometimes with this bristle. Abdomen normally black, sometimes partially yellow 13

13. Frons dark 14

Frons yellow 15

14. First flagellomere yellow. Fronto-orbital plate raised above frons. Epandrium with only a single spine at hind corner (as in Fig. 17) .... ***Liriomyza*** Mik, in part

1 sp., *galiivora* Spencer; western Canada; Spencer 1969

First flagellomere black (yellow only in *C. meridiana* Hendel from Central America and West Indies). Fronto-orbital plate in same plane as frons. Epandrium with conspicuous patch of spines at hind corner (as in Fig. 16) .... ***Calycomyza*** Hendel, in part

1 sp., *obscura* Spencer & Stegmaier; Florida; Spencer and Stegmaier 1973

15. Presutural dorsocentral bristle absent 16

Presutural dorsocentral bristle present 17

16. Anepisternum and femora mainly black. Epandrium with conspicuous patch of spines at hind corner (Fig. 16) .... ***Calycomyza*** Hendel, in part

31 spp.; Canada to Mexico; Spencer 1969, Spencer and Stegmaier 1973

Anepisternum, femora, and antenna entirely bright yellow. Epandrium without spines at hind corner .... ***Amauromyza*** Hendel, in part

1 sp., *A.* (*Catalpomyza*) *pleuralis* Melander; Spencer 1977

17. Antenna and legs black .... ***Amauromyza*** Hendel, in part

1 sp., *A.* (*Trilobomyza*) *flavifrons* Meigen; Spencer 1969

Antenna and legs yellow .... ***Phytoliriomyza*** Hendel, in part

1 sp., *hilarella* Zetterstedt; Canada to Florida; Spencer 1969

18. Fronto-orbital plate broad, raised above plane of frons; at least fronto-orbital plates dark .... ***Metopomyza*** Hendel

3 spp.; Canada, northern U.S.A.; Spencer 1969, Sehgal 1971

Fronto-orbital plate largely in plane of frons; entire frons yellow 19

19. Crossvein dm-cu absent. One reclinate orbital bristle present .... ***Haplomyza*** Hendel
4 spp.; Canada to Mexico; Spencer 1969, Spencer and Stegmaier 1973

Crossvein dm-cu usually present (absent in *Liriomyza singula* Spencer). Normally two reclinate orbital bristles present 20

20. Prescutellar area yellow. Fronto-orbital setulae usually upright or slightly proclinate, rarely slightly reclinate. Stridulating mechanism absent. Aedeagus with distinctive sclerotized paired sperm ducts (Fig. 15); epandrium with a conspicuous comb-like arrangement of black spines (Fig. 15) .... ***Phytoliriomyza*** Hendel, in part
3 spp.; Canada, northern U.S.A.; Spencer 1969

Prescutellar area usually dark, concolorous with mesonotum, rarely yellow. Fronto-orbital setulae distinctly reclinate. Stridulating mechanism always present (Figs. 13, 14). Aedeagus variable, normally pale, scarcely sclerotized, never with black tubules as in Fig. 15; epandrium with hairs along inner margin, never with a black comb-like process .... ***Liriomyza*** Mik, in part
66 spp.; Canada to Mexico; Spencer 1969, Sehgal 1971, Spencer and Stegmaier 1973

21. Costal section between R_1 and R_{2+3} usually at least twice length of section between R_{4+5} and M_{1+2}; crossvein dm-cu present or absent; crossvein r-m well distal to crossvein bm-cu (Fig. 11) .... ***Paraphytomyza*** Enderlein
6 spp.; Canada, northern U.S.A.; Spencer 1969

Costal section between R_1 and R_{2+3} conspicuously short, less than one-and-a-half times length of section between R_{4+5} and M_{1+2}; crossvein dm-cu absent; crossvein r-m close to or in line with crossvein bm-cu (Fig. 12) .... ***Pseudonapomyza*** Hendel
2 spp.; Canada to Mexico; Spencer 1969

22. C extending to M_{1+2} .... ***Phytoliriomyza*** Hendel, in part
5 spp.; Canada to Florida, Mexico; Spencer 1969

C extending only to R_{4+5} 23

23. Distal section of aedeagus simple, not bifid, lying below a lobe on dorsal side of aedeagus. Crossvein dm-cu usually absent, but present in two species in Europe .... ***Chromatomyia*** Hardy
26 spp.; Alaska to Mexico; Griffiths 1974*a*

Distal section of aedeagus bifid, without such lobe above. Crossvein dm-cu present or absent 24

24. Crossvein dm-cu usually present, close to or in line with crossvein r-m (Fig. 10); if crossvein dm-cu absent, male terminalia with remnant of pregenital segment present; costal section between R_1 and R_{2+3} not more than twice length of section between R_{4+5} and M_{1+2} (Fig. 10). Frons always strongly projecting .... ***Napomyza*** Westwood
11 spp.; northern Canada to Mexico; Spencer 1969

Crossvein dm-cu normally absent; if this crossvein present, costal section between R_1 and R_{2+3} two-and-a-half times length of section between R_{4+5} and M_{1+2} and frons not projecting, e.g. *davisii* (Walton) and *parvicella* (Coquillett) .... ***Phytomyza*** Fallén
122 spp.; Alaska to Mexico; Spencer 1969, Sehgal 1971, Griffiths 1972*c et seq.*

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74

OPOMYZIDAE

J. R. Vockeroth

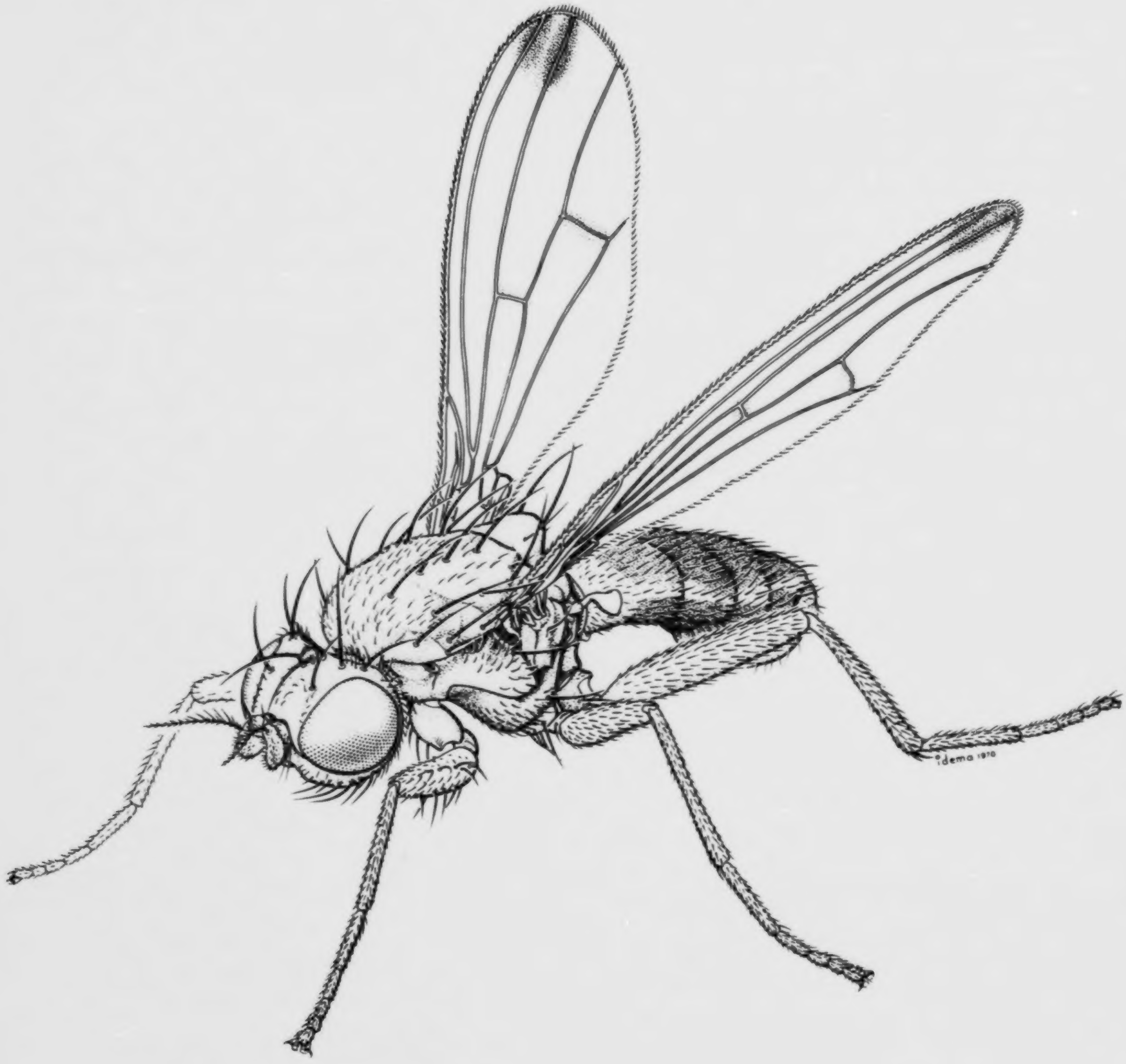


Fig. 74.1. Male of *Geomyza lurida* (Loew).

Slender to very slender flies (Fig. 1), 2.0–4.4 mm long, shining to pruinose yellow, reddish, brown, or blackish. Wing always with at least an apical spot, usually with more extensive markings.

Adult. Head (Figs. 2, 3): frons slightly narrowed anteriorly; frontal vitta more weakly sclerotized, slightly depressed, strongly narrowed anteriorly, margined by minute hairs. Face with a weakly sclerotized narrow triangular median area that extends dorsally almost to antennae; lateral portion of each side more strongly sclerotized than the rest, and with a very shallow antennal groove; parafacial very narrow, especially above. Gena about one-fifth height of eye; clypeus small but distinct. Upper half of postcranium concave. One strong orbital bristle present, a little above middle of frons at anterior end of a distinct or obscure oblique orbital plate; ocellar and inner and outer vertical bristles strong; postocellar bristles usually absent, but if present, divergent; one or two more or less regular rows of subvibrissal setulae present below eye; sometimes one or more subvibrissal setulae enlarged and bristle-like but no vibrissa present on the obscure vibrissal angle. Eye with very short sparse hairs. Antenna short; first flagellomere produced downward and distinctly pubescent; arista pubescent, with dorsal hairs often much longer than ventral ones. Proboscis short; labella large, fleshy; palpus moderately large, broadened.

Thorax: scutum strongly bristled, with one postpronotal, one presutural supra-alar, two notopleural, one supra-alar, one strong and one weak postalar, one presutural dorsocentral, and two or three postsutural dorsocentral bristles; acrostichal hairs very short, appressed, in about four to ten irregular rows; scutellum haired or bare above, with four bristles, the basal pair usually weak; anepisternum posteriorly with many hairs and one strong bristle; anepimeron with a few hairs, rarely with a weak bristle; katepisternum with a strong bristle. Prosternum haired, slightly to strongly broadened anteriorly, not fused with propleuron. Metasternal area broad throughout, bare.

Wing (Figs. 4–7) moderately broad to extremely narrow. Alula and anal lobe often absent. Cells of posterior half of wing narrow. C broken only at apex of Sc, and extending to end of M; Sc incomplete, extremely weak on apical half; R_1 with a weak upward projection at level of subcostal break; cell dm and cell bm usually incompletely separated; cell cu*p* present, small; A_1 either present and incomplete, or absent.

Legs weakly bristled (Fig. 1). Tibiae without dorsal preapical bristle; mid tibia with long strong ventral bristle at apex.

Abdomen: six pairs of spiracles located in membrane below corresponding tergites or, in male of *Opomyza* Fallén and *Geomyza* Fallén, sixth pair in membrane behind or above posteroventral corners of tergite 5 (Fig. 10).

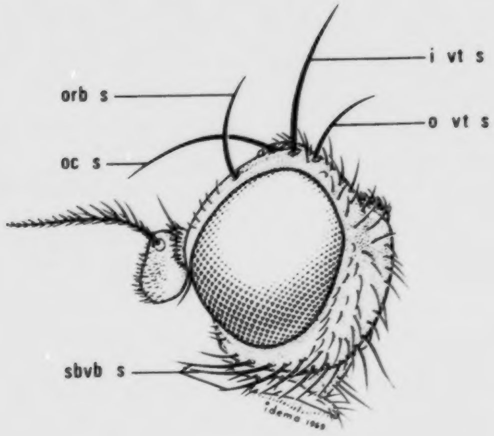
Male of *Opomyza* and of *Geomyza* (Fig. 10) without tergite 6, with only one segmental complex between segments 5 and 9; this complex consisting of a short bare sternite 6 displaced to the left, a small to large bare sternite 7 on left side of abdomen, and a large haired dorsal and nearly symmetric remnant of segment 8; male of *Anomalochaeta* Frey with a narrow bare free tergite 6 lying behind tergite 5, and with remnants of segments 6–8 as in other two genera. Epandrium, hypandrium and associated structures, and cerci all symmetric in structure and position. Epandrium short, produced ventrally on each side into a short or moderately long tapering process that probably represents a fused surstylus; each process with only the anteroventral portion of inner surface sclerotized and haired, and usually with the apex produced into a short spur or with short stout spines on inner surface. Hypandrium deep, with lateral and submedian margins extended dorsally, and with the two halves joined anteroventrally and also posterodorsally by a narrow bridge; each submedian margin near anterior end with a slender dorsal arm (aedeagal guide) that is attached to the aedeagal apodeme; gonopod fused with hypandrium, its position represented by a group of setae along submedian margin of hypandrium; paramere represented by a slender weak sclerite bearing several setulae and lying between base of aedeagus and inner posterior margin of gonopod; aedeagus heavily sclerotized, long, stout, complex, not coiled, of somewhat different form in each genus but with only slight specific differences; epiphallus replaced by a complex process, hinged in the middle, and united anteriorly to posterior margin of basiphallus, posteriorly with hypandrial bridge, and laterally with parameres; aedeagal apodeme long, slender throughout or with anterior end spatulate. Cerci slender, elongate, closely joined by membrane on about basal half but with apical half of each cercus subcylindrical or slightly flattened and curved, with many setae, and projecting ventrally about as far as apex of surstylar process.

Female (Fig. 11) with abdominal tergites and sternites 1–7 well-developed, not fused. Segment 8 and cerci slightly compressed but not heavily sclerotized, separated from segment 7 by an extensive membrane; tergite 8 divided, weak; sternite 8 entire, weak medially or divided. Hypoproct and epiproct not present as separate sclerites. Cercus two to five times as long as wide, sometimes with epiproct and cercus fused to apex of half of tergite 8. Two sclerotized spermathecae present, subspherical or elongate.

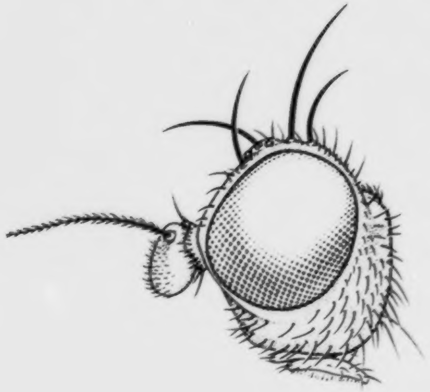
Larva. Slender, cylindrical, smooth except for ventral zones of fine spicules on all segments and for dorsal zones of spicules on thoracic segments and, at most, on first five abdominal segments. Facial mask with several concentric rows of rounded closed cells, each cell usually bearing from one to four pointed spicules; mandible heavy, with three to five small teeth following apical tooth; dental sclerite undivided, crescentic or V-shaped; hypopharyngeal sclerite fused with tentoropharyngeal sclerite; whole cephalopharyngeal skeleton densely tanned except for tip of ventral wing. Anterior spiracles of rosette or branched type, with 6–16 papillae (Figs. 8, 9); posterior spiracles on large weakly or distinctly separated lobes; each posterior spiracle with three short oval radially arranged slits and with four groups of branched interspiracular hairs (Hennig 1952, Nye 1958).

Biology and behavior. The few species whose larvae are known feed in grass stems. Some are of minor economic importance in Europe but none have been so reported in North America.

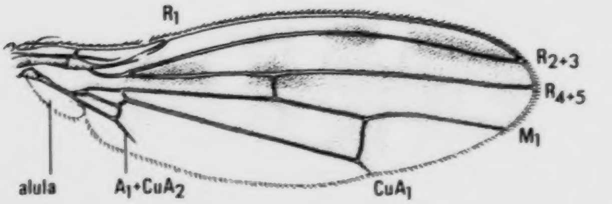
Classification and distribution. Hennig (1971) referred the Opomyzidae to the superfamily Anthomyzoidea and suggested a sister-group relationship with the family Anthomyzidae. Many genera have been referred to the family but apart from the three treated in the key below only *Scelomyza* Séguy from Kenya is likely to belong here. About 40 species of the family are known; most occur in the Holarctic region but a few are in the mountains of eastern and southern Africa (Stuckenberg 1963). Three Nearctic species, including both species of *Opomyza*, are undoubtedly immigrants from the Palaearctic; more species are likely to enter. Vockeroth (1961) has treated the Nearctic species. No fossil species are known.



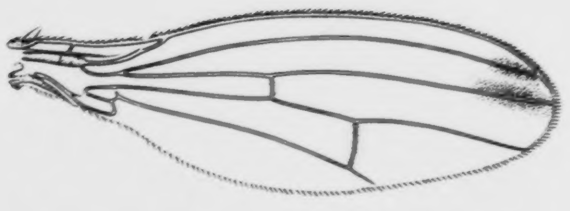
2 Geomyza lurida ♂



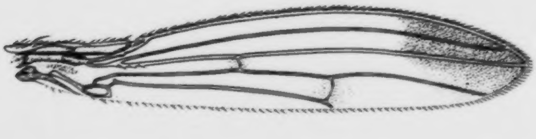
3 Opomyza petrei ♂



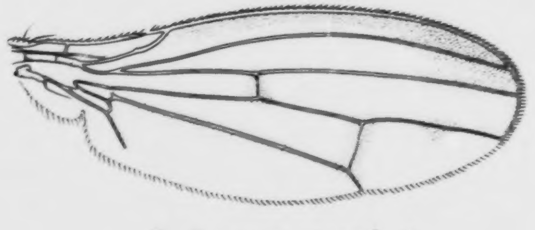
4 Anomalochaeta guttipennis ♂



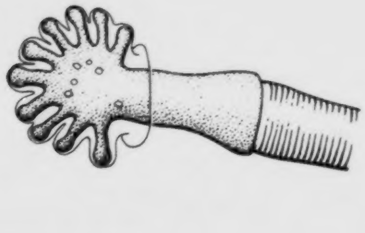
5 Geomyza lurida ♂



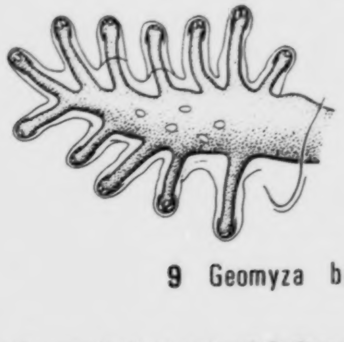
6 Geomyza apicalis ♂



7 Opomyza petrei ♂



8 Opomyza petrei



9 Geomyza balachowskyi

Figs. 74.2–9. Heads, wings, and larval spiracles: head of (2) *Geomyza lurida* (Loew) and (3) *Opomyza petrei* Mesnil; wing of (4) *Anomalochaeta guttipennis* (Zetterstedt), (5) *Geomyza lurida*, (6) *Geomyza apicalis* (Meigen), and (7) *Opomyza petrei;* anterior spiracle of larva of (8) *Opomyza petrei* and (9) *Geomyza balachowskyi* Mesnil.

Abbreviations: i vt s, inner vertical seta; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; sbvb s, subvibrissal seta.

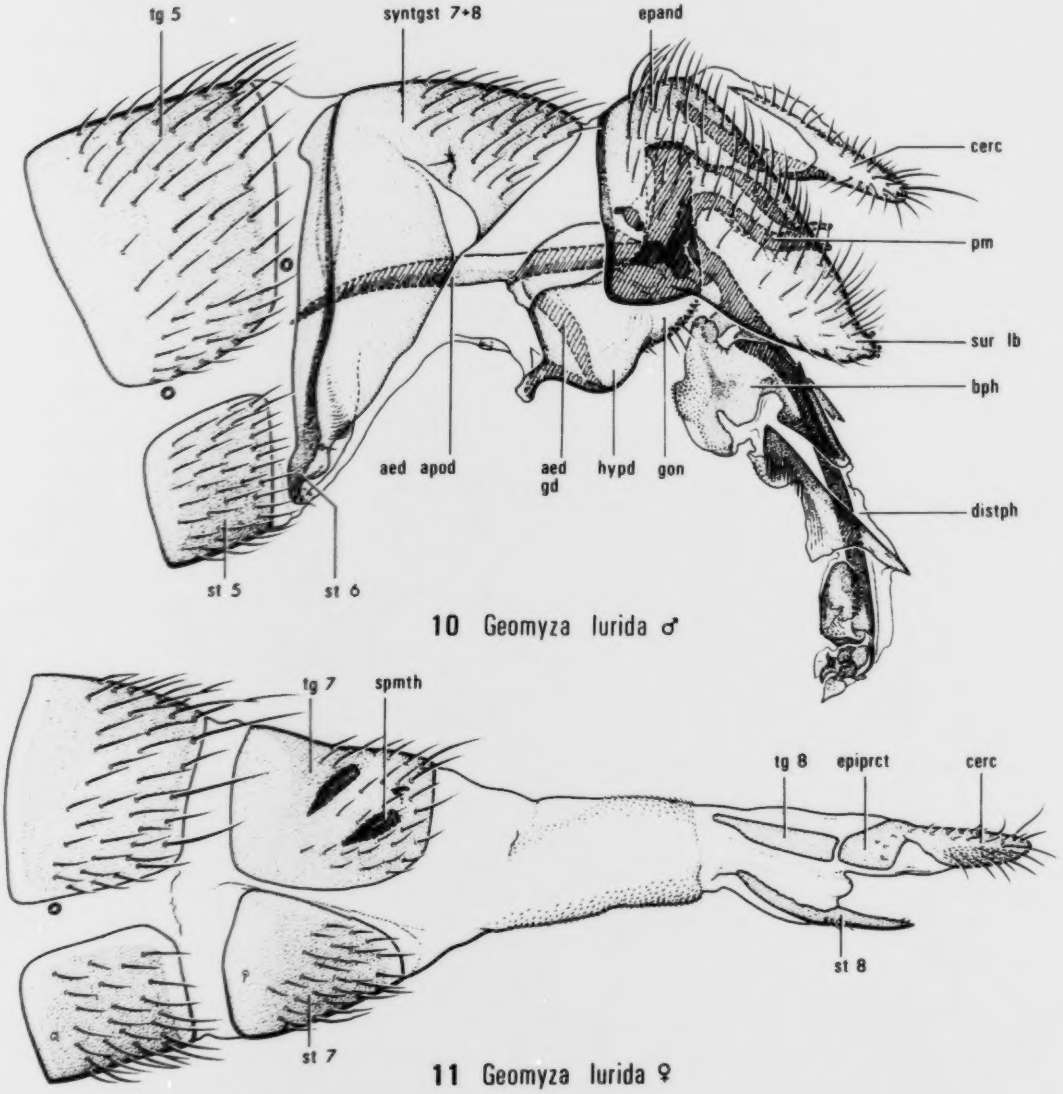
Keys to genera

Adult

1. Postocellar bristles present. Wing (Fig. 4) mostly dark, with about 10 rounded hyaline spots .... ***Anomalochaeta*** Frey

   1 sp., *guttipennis* (Zetterstedt); boreal

   Postocellar bristles absent. Wing (Figs. 2–4) mostly clear, with costal margin and some veins darkened, or with only apex and crossveins darkened 2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10 Geomyza lurida ♂

11 Geomyza lurida ♀

Figs. 74.10–11. Terminalia of *Geomyza lurida* (Loew): (10) male and (11) female.
Abbreviations: aed apod, aedeagal apodeme; aed gd, aedeagal guide; bph, basiphallus; cerc, cercus; distph, distiphallus; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; pm, paramere; spmth, spermatheca; st, sternite; sur lb, surstylar lobe; syntgst, syntergosternite; tg, tergite.

2. Alula and anal angle obsolete; wing often markedly reduced in size (Figs. 5, 6). Disc of scutellum bare; basal scutellar bristles very short. Arista long-haired above, short-haired below. One or more subvibrissal hairs enlarged, vibrissa-like (Fig. 2) .... ***Geomyza*** Fallén
10 spp.; widespread

Alula and anal angle well-developed; wing not reduced in size (Fig. 7). Disc of scutellum haired; basal bristles subequal to apical bristles. Arista pubescent. Subvibrissal setulae all short and fine (Fig. 3) .... ***Opomyza*** Fallén
2 spp.; widespread

Larva

(adapted from Nye 1958)

1. Anterior spiracles of rosette type (Fig. 8); ventral abdominal spicular zones not divided by a distinct gap into anterior and posterior rows .... ***Opomyza***

Anterior spiracles of branched type (Fig. 9); two to eight ventral abdominal spicular zones each divided by a distinct gap into anterior and posterior rows .... ***Geomyza***

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ANTHOMYZIDAE

75

J. R. VOCKEROTH

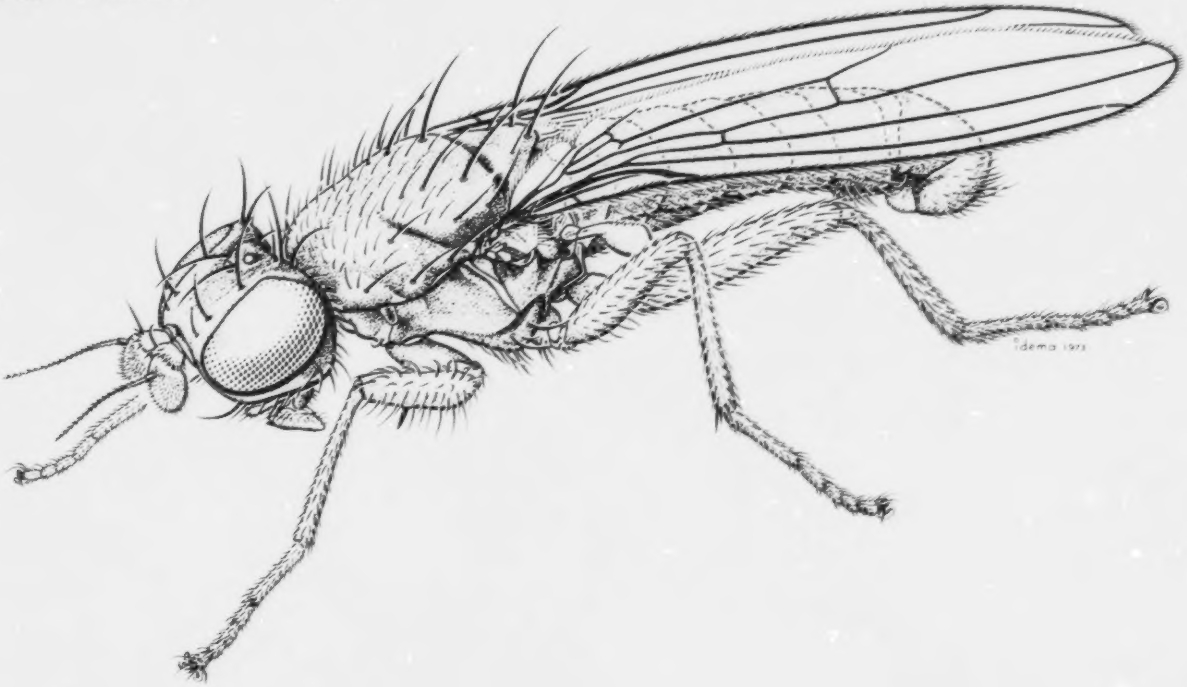


Fig. 75.1. Male of *Anthomyza gracilis* Fallén.

Very slender flies (Fig. 1), 2.0–3.0 mm long, shining to moderately pruinose, yellow to black, rarely with wing markings, very rarely with strongly reduced wings.

Adult. Head (Fig. 2): Frons slightly narrowed anteriorly; interfrontal area slightly weaker; fronto-orbital plates narrow, entire; ocellar triangle usually large and well-defined. Face usually depressed; parafacial narrow to rather broad. Gena at most one-tenth height of eye; clypeus small but distinct. Upper half of postcranium slightly concave. One to three orbital bristles present, the anterior one weak or absent, all slightly reclinate; ocellar and inner and outer vertical bristles present, usually strong; postocellar bristles short, weak, and convergent, absent in some exotic species; a row of very weak genal hairs present below eye, ending anteriorly in one or two distinct vibrissa-like bristles. Eye bare. Antenna short; first flagellomere turned downward, rounded apically, and distinctly pubescent; arista with very short to long hairs. Proboscis short; labella large, fleshy; palpus long, moderately heavy.

Thorax: Postpronotum with one bristle. Scutum with two notopleural, sometimes one presutural intra-alar, one supra-alar, one postalar, and sometimes two postsutural dorsocentral bristles; acrostichal hairs fine, in two to four fairly regular rows. Scutellum bare above, with two short subbasal and two long apical bristles. Katepisternum with two dorsal bristles and several ventral hairs; other pleural sclerites bare. Prosternum bare, strongly broadened anteriorly, not fused with propleuron. Metasternal area moderately large, bare.

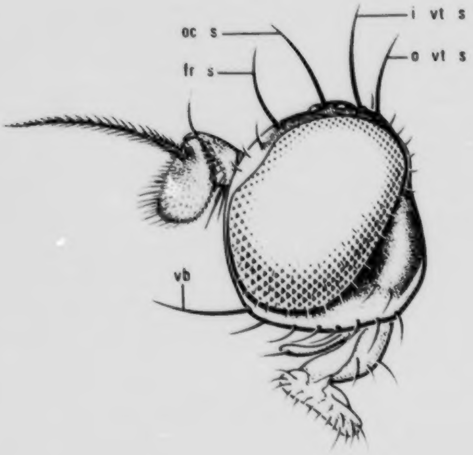
Wing usually well-developed but rather slender (Fig. 4), sometimes reduced to as little as one-third its normal length and width, acute apically, and with very reduced venation (Fig. 3). In normal wing, C with only subcostal break, extending to apex of M; Sc weak, obsolete on apical one-third; cells bm and dm incompletely separated; cell cu*p* entire; A_1 strong, straight, not reaching wing margin. Alula narrow. Halter well-developed or rudimentary, usually entirely pale.

Abdomen: tergites and sternites 1–5 unmodified; tergite 1 free, about one-half as long as tergite 2. Spiracles 1–5 situated in membrane below tergites.

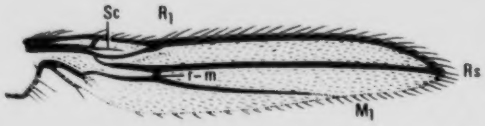
Male (Figs. 6, 7) with tergite 6 from one-fifth to one-tenth as long as tergite 5, bare; sternite 6 short, asymmetric, produced upward on left side, and fused with tergite 7. Sternite 7 on left side of abdomen, haired, fused with sternite 8. Sternite 8 dorsal, large, haired, slightly asymmetric. Spiracle 6 situated in membrane below tergite 6; left spiracle 7 situated in anterior margin of sternite 7; right spiracle 7 situated in membrane below tergite 6. Epandrium small, slightly or deeply excavated posteriorly, with a rather slender tapering surstylus articulated at each posteroventral angle. Hypandrium rather shallow, surrounding base of aedeagus, anteriorly with a dorsal process on each side fused with aedeagal apodeme, the two processes forming the aedeagal guide. Gonopod fused with hypandrium, represented by a compressed triangular process with a few apical hairs. Parameres complex, usually subdivided. In *Anthomyza* Fallén (see Anderson 1976, Fig. 1) each paramere consisting of a narrow strap-like sclerite connecting gonopod to basiphallus and an anterolateral spinulose lobe at base of aedeagus; a heavily sclerotized serrate median lobe (unpaired) present between their bases ("epiphallus" of Anderson 1976 and Griffiths 1972). In *Mumetopia* Melander (Fig. 7) each paramere consisting of a large exposed lateral lobe and an unexposed anterolateral lobe which is spinulose on its inner face; an exposed finger-like lobe present posteriorly (unpaired). Aedeagus complex and asymmetric, consisting of a short swollen basal portion and an elongate mostly slender apical portion that sometimes bears a sac-like process with heavy external spines about midway and a slender filament at the apex; aedeagal apodeme long, strong, moderately heavy; ejaculatory apodeme relatively small. Cerci small, weakly sclerotized.

Female (Figs. 8, 9) with segment 6 unmodified; spiracle 6 situated below margin of tergite. Tergite 7 and sternite 7 separate or fused into a ring; this ring rather heavily sclerotized or weakened on ventral surface; spiracle 7 situated below tergite 7 or enclosed in the ring sclerite. Tergite 8 small, sometimes with anterolateral arms or a posteromedian process; sternite 8 at most as long as tergite 8, divided medially, with each half slightly to strongly compressed and bluntly rounded apically. Genital chamber with a weak to moderately strong sclerite on lateral wall and sometimes with a median loop-like slender sclerite; chamber exsertable under pressure in macerated specimens but perhaps not in living ones. Hypoproct very small, nearly flat; epiproct larger, convex below; cercus slender, two to three times as long as wide. Spermathecae two in number, subspherical to subcylindrical, strongly sclerotized.

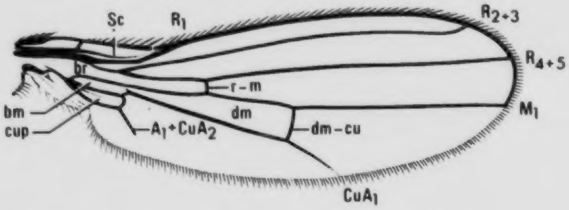
Larva. Slender, subcylindrical, smooth except for ventral zones of fine spicules on all segments and for dorsal zones on last two thoracic and first seven abdominal segments. Head distinctly emarginate anteriorly; facial mask with oblique comb-like rows of apically rounded denticles; mandible slender, sickle-shaped, with very small ventral teeth; dental sclerites paired, very small; hypopharyngeal sclerite long and slender, not fused with tentoropharyngeal sclerite; tentoropharyngeal sclerite deeply divided, with slender dorsal cornu and robust ventral cornu; whole cephalopharyngeal skeleton rather lightly tanned, especially ventral cornu. Anterior spiracle palmate with three to six digitations (Fig. 5)



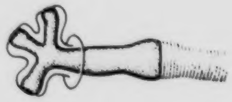
2 Mumetopia occipitalis ♂



3 Anthomyza sabulosa ♂



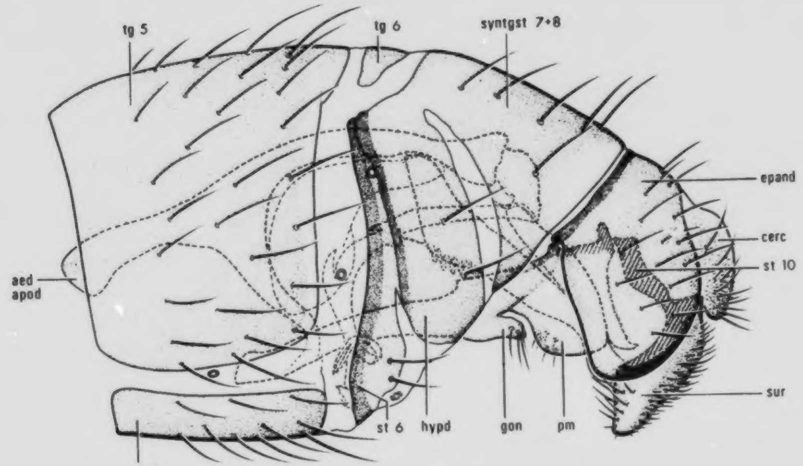
4 Anthomyza gracilis ♂



5 Anthomyza sabulosa

Figs. 75.2-5. Head, wings, and larval spiracle: (2) head of *Mumetopia occipitalis* Melander; (3) wings of *Anthomyza sabulosa* Haliday and (4) *Anthomyza gracilis* Fallén; (5) anterior spiracle of larva of *Anthomyza sabulosa*.

Abbreviations: fr s, fronto-orbital seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s , outer vertical seta; vb, vibrissa.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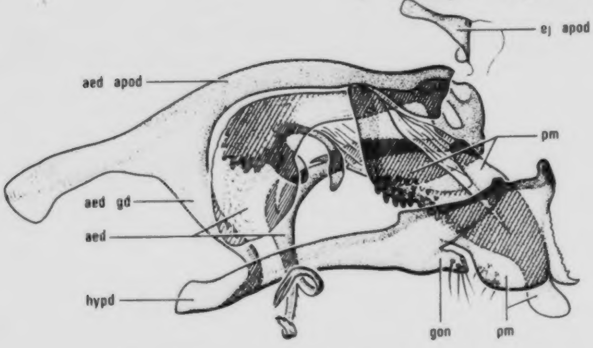
6 Mumetopia occipitalis ♂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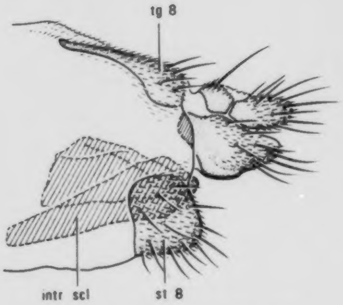
7 Mumetopia occipitalis ♂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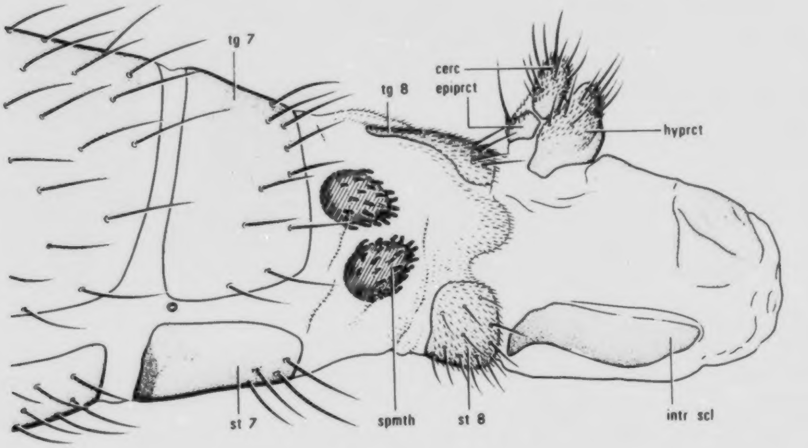
8 Mumetopia occipitalis ♀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9 Mumetopia occipitalis ♀

Figs. 75.6–9. Male and female terminalia of *Mumetopia occipitalis* in lateral view: (6) male terminalia; (7) hypandrium and associated parts; (8) apex of female terminalia; (9) female terminalia with genital chamber exserted.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct: intr scl, internal sclerite; pm, paramere; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

or pinnate with five lateral digitations. Posterior spiracles on small widely spaced lobes; each spiracle with four groups of fine branched hairs (Hennig 1952, Nye 1958).

Biology and behavior. The few known larvae feed in grass stems but seem to be of little economic importance; it has been suggested that they may be saprophagous rather than phytophagous. Adults are often abundant in moist grassy areas.

Classification and distribution. The Anthomyzidae are almost certainly closely related to the Opomyzidae but whether they are sister groups, as Hennig (1971) has suggested, is not yet clear. The family limits are still doubtful. Several genera recently referred to the family, such as *Stenomicra* Coquillett (widespread) (included in the Aulacigastridae in this Manual), *Melananthomyza* Malloch (Chile), and *Waterhouseia* Malloch (Australia), probably do not belong here. The three Nearctic genera recognized here, plus several exotic genera such as *Paranthomyza* Czerny, *Anagnota* Becker, and *Amygdalops* Lamb, form a very compact and undoubtedly monophyletic group. The genera have been based mostly on slight differences in antennal shape, head bristling, and venation; a revision of the genera would be desirable, considering particularly the structures of the terminalia. The Nearctic species are mostly undescribed. In the large genus *Anthomyza* two Holarctic and three Nearctic species have been recorded from North America. However, Andersson (1976) has shown that several European species have been incorrectly identified and that a revision of the Holarctic fauna is needed.

The family in the restricted sense occurs in all continental areas. In the north it extends to the limit of trees.

Three fossil genera, with a total of four species, have been described from Baltic amber (Hennig 1965, 1967, 1969). However, it is not certain that all three genera should be included in the Anthomyzidae.

Key to genera

1. Fronto-orbital plates with one pair of strong bristles (Fig. 2)........ ***Mumetopia*** Melander
   3 spp.; eastern
   Fronto-orbital plates with two pairs of strong bristles 2
2. Crossvein dm-cu situated about its own length from wing margin; wing well-developed .... ***Ischnomyia*** Loew
   2 spp.; eastern
   Crossvein dm-cu situated about twice its own length from wing margin (Fig. 4) or wing moderately or greatly reduced (Fig. 3) .... ***Anthomyza*** Fallén
   5 spp.; widespread

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AULACIGASTRIDAE

76

H. J. TESKEY

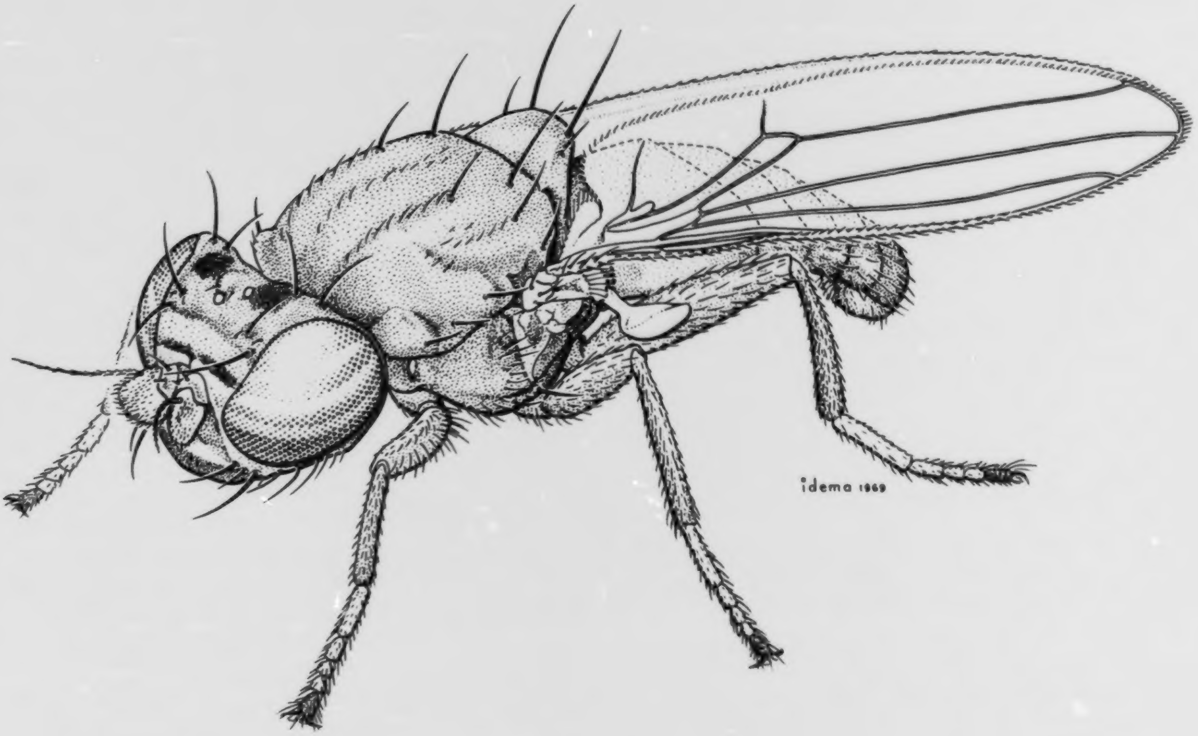


Fig. 76.1. Male of *Aulacigaster leucopeza* (Meigen).

Small flies, 2.5–5 mm long, moderately broad to slender (Fig. 1), dark brown to predominantly yellowish. Lower facial margin receding. Wing hyaline or with infuscated markings.

Adult. Head: broader than thorax, broader than high, and usually short (Figs. 1–3), but elongate and dorsoventrally compressed in several exotic species. Compound eye usually conspicuously pubescent; anteroventral portion of each eye impinging on face and with enlarged ommatidia (Figs. 2, 3). Postcranium dorsally concave. Frons rather broad, parallel-sided to slightly narrowed or widened below. Face more or less strongly narrowed near its middle at vibrissal angles, somewhat projecting or with a raised transverse ridge at or below constriction, strongly receding to lower facial margin. Chaetotaxy: two orbital bristles present, lower one usually pointed inwardly and situated more or less laterally of upper bristle; ocellar bristles usually absent, but when present, weak; postocellar bristles absent or minute; outer, and usually inner, vertical bristles present and strong; no distinct vibrissae, but sometimes one or more of subvibrissal row of bristles enlarged and resembling vibrissae; face sparsely setose medially in exotic *Planinasus* Cresson. Antenna short; first flagellomere oval to round, situated terminally on pedicel or somewhat lengthened and pendulous from pedicel; arista with one to three aristomeres and with very short hairs (Fig. 1), or with long plumules (Figs. 2, 3), of which dorsal plumules are longer than ventral ones, and ventral plumules are restricted to apical half. Proboscis fleshy and retractile; palpus usually small, oval to round, pale.

Thorax: Subscutellum usually well-developed. Chaetotaxy: two notopleural, one postalar, one postsutural supra-alar, and one or two postsutural dorsocentral bristles present (Fig. 1); sometimes one postpronotal bristle present; supra-alar and dorsocentral bristles preceded by a row of short setulae; one or two rows of small acrostichal setulae present; scutellum with two or four bristles, of which the basal pair is often weaker; anepisternum usually with several setulae and one strong bristle in a row posteriorly; katepisternum with one or two bristles, of which the posterior bristle is strongest.

Wing (Fig. 1) longer than body, moderately wide, hyaline or infuscated; infuscation, when present, situated along costal border in diffuse median or apical crossbands or both, or occurring more extensively, with hyaline areas particularly over crossveins and at wing base. Alula and anal lobe usually well-developed. C extending to M_{1+2}, weakly broken at end of Sc; Sc incomplete, sometimes fused with R_1 for a short distance, but apical section fading before reaching C shortly before subcostal break; R_1 ending near subcostal break; following three veins ending in apical quarter of wing; cells bm and dm sometimes separated; cell cu*p* present or absent; A_1 extending about half distance to wing margin.

Legs weakly bristled; mid tibia usually with apicoventral bristle. Preapical dorsal bristles present only in *Planinasus.*

Abdomen: oval to oblong, as wide as or slightly wider than thorax, and dorsally somewhat flattened. Tergites rather shiny; at least six tergites clearly visible from above in both sexes. Seven pairs of spiracles situated in membrane in both sexes.

Male terminalia in *Aulacigaster* Macquart (Fig. 5) with dorsal parts of pregenital segments relatively symmetric. Hypandrium with a strong lateral apodeme arising anteriorly at base of each gonopod, and with a relatively large platelike hypandrial bridge posteriorly; gonopods large, with spinous cushion subapically; parameres simple; aedeagus with very large ejaculatory apodeme and cuneiform aedeagal apodeme. Cerci well-developed; surstylus each represented by a short slender lobe from epandrium. In *Stenomicra* Coquillett and *Cyamops* Melander remnants of segments 6–8 quite asymmetric, with asymmetry extending to epandrium and large prominent surstyli in *Cyamops; Cyamops* with very complex aedeagus having a slender aedeagal apodeme and unusually large angled ejaculatory apodeme.

Female terminalia (Fig. 4) short, with fusion of tergites and sternites of segments 6 and 7 in *Cyamops* and of segment 8 in *Stenomicra.* Cercus normally pointed, with strong terminal setae. Three spermathecae present in *Aulacigaster* and *Cyamops,* two in *Stenomicra.*

Larva. Only that of *Aulacigaster leucopeza* (Meigen) (Fig. 6) adequately described; slender, subcylindrical, amphipneustic, with long partially retractile terminal respiratory tube. Cephalopharyngeal skeleton slender, typical of many Muscomorpha; mandible small; hypopharyngeal and tentoropharyngeal sclerites separate.

Integument covered with minute spicules. Abdominal segments with prominent paired ventral creeping welts bearing spicules arranged in one row on segments 1 and 8 and in two rows on remaining segments. Anal pad large, bilobate. Anterior spiracle a long retractile filament with openings sessile along its length; posterior spiracles distinctly separated on end of respiratory tube, each with three small projecting papillae.

Biology and behavior. Larvae of *Aulacigaster leucopeza* inhabit fermenting sap exuding from wounds on a wide variety of trees (Malloch and McAtee 1924, Robinson 1953). They apparently are not injurious to the tree.

No further biological information on representatives of the family is known, although Sabrosky (1975) points out that the frequency with which several species of *Stenomicra* have been recorded as swept from grasses may be significant.

Classification and distribution. Hennig (1969, 1971), by transfer from other families, has increased to five the number of genera currently placed in the Aulacigastridae. These are *Aulacigaster, Cyamops, Planinasus, Stenomicra,* and *Schizochroa* Hennig. They include 25 species from all faunal regions, almost half belonging to the genus *Stenomicra.* Three genera and five species are represented in the Nearctic region.

The family placement of *Stenomicra* is controversial: Hennig (1969) transferred it from the Anthomyzidae but Griffiths (1972), based largely on features of the male terminalia, thought it should remain in the Anthomyzidae.

One fossil species from Baltic amber placed in the Aulacigastridae (Hennig 1965) is *Protoaulacigaster electrica* Hennig. Another Baltic amber species, *Xenanthomyza larssoni* Hennig, was compared with *Stenomicra,* which at that time Hennig placed in the Anthomyzidae (Hennig 1967).

Key to genera

1. Ocellar hairs present. Arista with very short hairs. Face and lower frons prominently banded in white, brown, and orange (Fig. 1) .... ***Aulacigaster*** Macquart

1 sp., *leucopeza* (Meigen); Holarctic

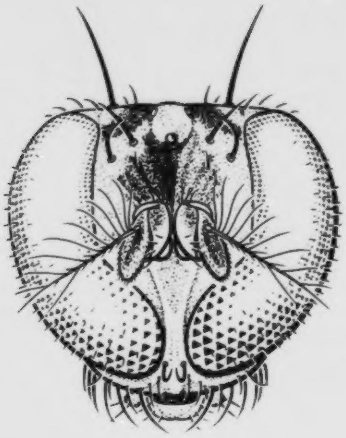
Ocellar hairs absent. Arista with long pectinate rays. Face and frons essentially unicolorous 2

2. Inner vertical bristles absent; middle of face constricted to less than half width between eyes at antennae (Fig. 2) .... ***Cyamops*** Melander

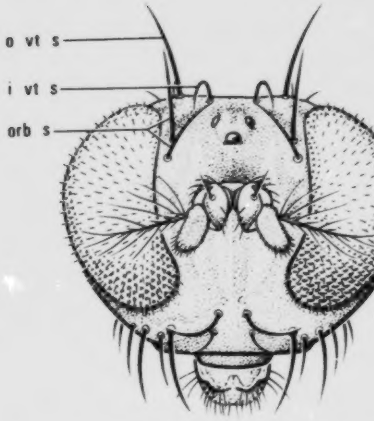
3 spp.; eastern; Sabrosky 1958

Inner vertical bristles present; narrowest part of face more than half width between eyes at antenna (Fig. 3) .... ***Stenomicra*** Coquillett

1 sp., *angustata* Coquillett; eastern



2 Cyamops nebulosus ♂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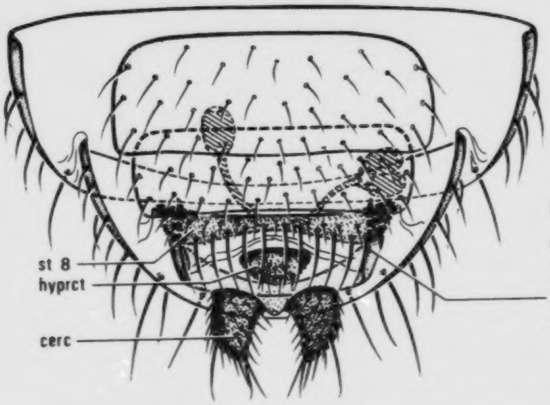
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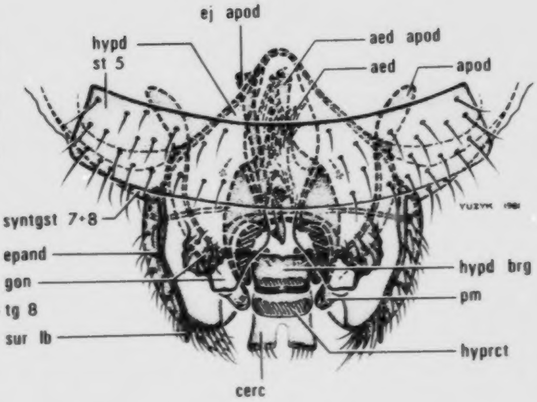
4 Aulacigaster leucopeza ♀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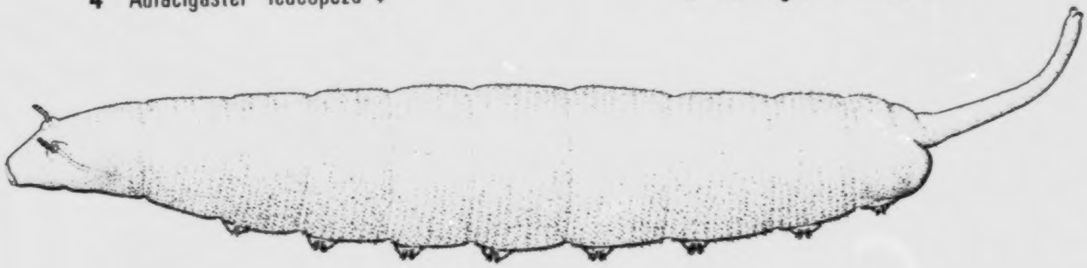
5 Aulacigaster leucopeza ♂



6 Aulacigaster leucopeza

Figs. 76.2–6. Heads, terminalia, and larva: anterior views of head of (2) *Cyamops nebulosa* Melander and (3) *Stenomicra angustata* Coquillett; dorsal views of (4) male terminalia and (5) female terminalia of *Aulacigaster leucopeza;* (6) larva of *Aulacigaster leucopeza*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; apod, apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; hypd brg, hypandrial bridge; hyprct, hypoproct; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; st, sternite; sur lb, surstylar lobe; syntgst, syntergosternite; tg, tergite.

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PERISCELIDIDAE

77

J. F. McAlpine

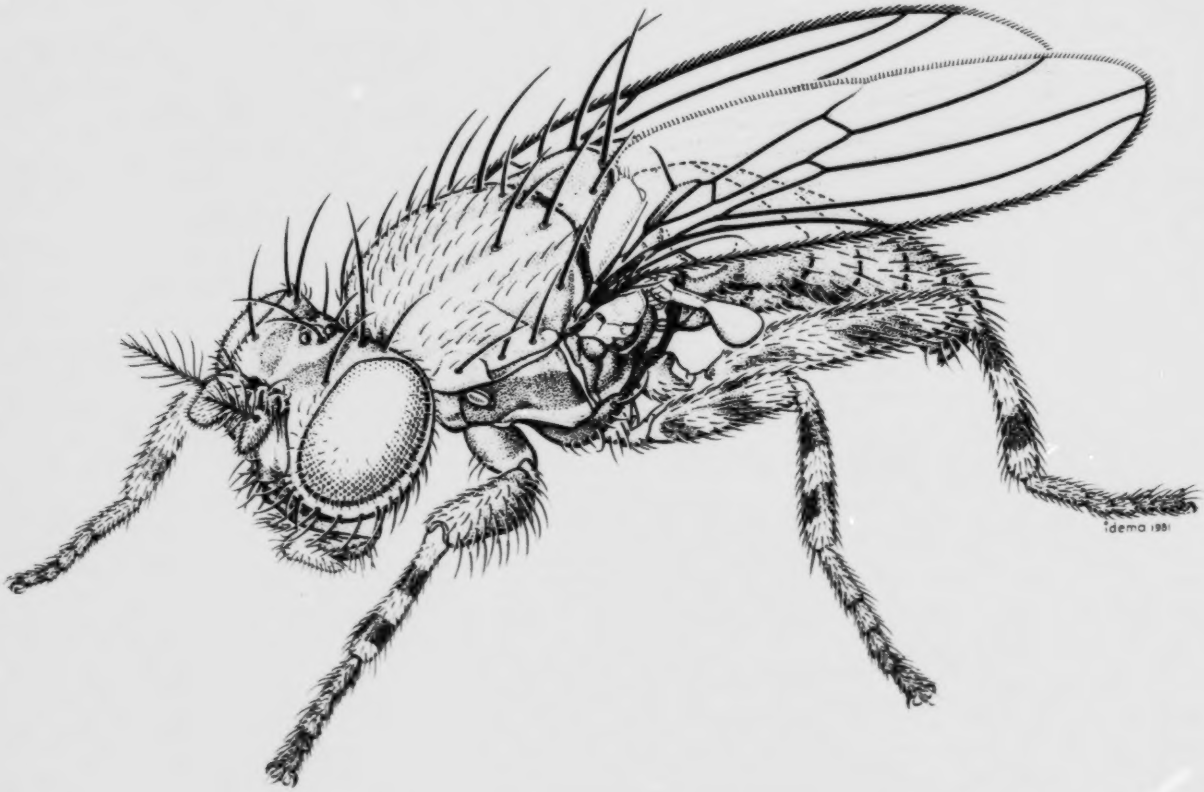
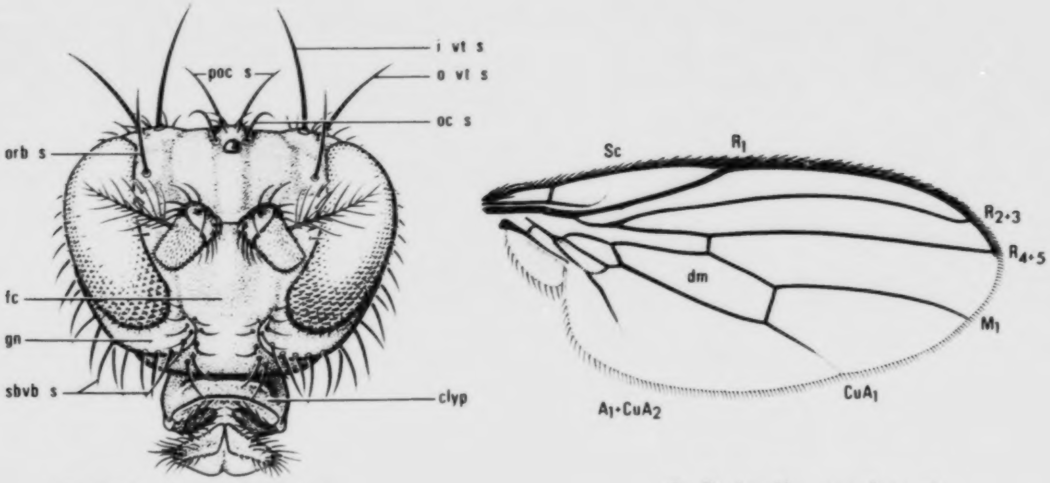


Fig. 77.1. Male of *Periscelis annulata* (Fallén).

Small drosophilid-like flies (Fig. 1), 3–4 mm long, dull grayish black or brownish black, with milky sometimes brownish-marked wings, and frequently with banded tibiae.

Adult. Head: at least as broad as thorax, distinctly broader than high (Fig. 2), and usually higher than long. Postcranium strongly concave above. Frons broader than high, becoming narrower toward bases of antennae; lunule linear, unexposed. Face strongly attenuated between anteroventral extremities of the eyes, usually with a raised plate- or tubercle-like swelling between vibrissal angles, not at all weakened along midline, frequently with hairs on lower portion. Clypeus moderately well-developed; cheek broad, rather strongly bulging posteriorly. Compound eye vertically oval, with short sparse pubescence. Chaetotaxy: one pair of moderately strong frontal, ocellar, inner vertical, outer vertical, and postocellar bristles present; postocellar bristles divergent; distinct vibrissa usually lacking, but a series of relatively strong subvibrissal bristles present along subcranial margin; only a few fine setulae on frons, restricted to lateral margins opposite bases of antennae. Antenna short; pedicel more or less swollen and cap-like, with a dorsal seam and with dorsal surface extended beyond base of first flagellomere as in most Drosophilidae (Fig. 2); first flagellomere only slightly longer than broad, strongly decumbent, meeting pedicel almost at right angles; arista plumose, with dorsal rays more numerous than ventral ones; two basal aristomeres very short. Proboscis moderately short and stout; palpus small to rather large; labella well-developed.

Thorax: usually grayish or brownish pruinose, usually with a brown pleural stripe running from in front of anterior spiracle to base of halter (Fig. 1). Disc of propleuron bare, usually with one or more proepisternal bristles, but these sometimes absent; proepimeral bristle absent; prosternum narrow, free from propleuron, bare. Scutum with rather sparse short setulae; one postpronotal bristle present; several postsutural dorsocentral, two notopleural, one postsutural supra-alar, and one postalar bristle present; prescutellar acrostichal bristles present or absent; scutellum moderately large and convex, sometimes slightly flattened on disc, with two pairs of bristles, usually without additional setulae, and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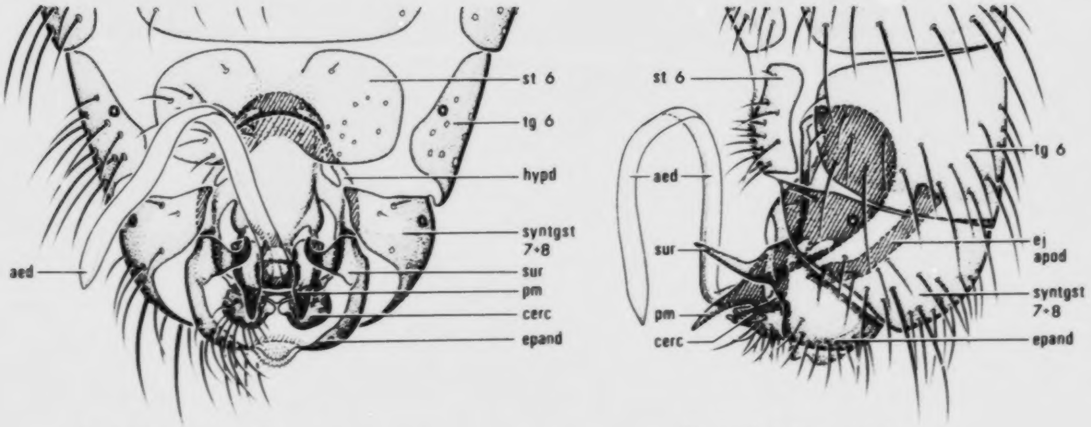
2 Periscelis annulata ♂

3 Periscelis annulata ♂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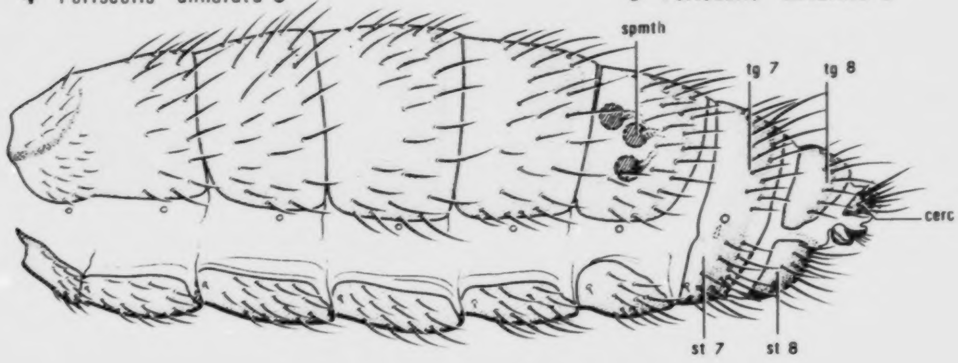
4 Periscelis annulata ♂

5 Periscelis annulata ♂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6 Periscelis annulata ♀

Figs. 77.2–6. *Periscelis annulata* (Fallén): (2) head, anterior view; (3) wing; (4) ventral and (5) left lateral views of male abdomen and terminalia; (6) left lateral view of female abdomen and terminalia.

Abbreviations: aed, aedeagus; cerc, cercus; clyp, clypeus; ej apod, ejaculatory apodeme; epand, epandrium; fc, face; gn, gena; hypd, hypandrium; i vt s, inner vertical seta; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; sbvb s, subvibrissal seta; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

with apical pair of scutellar bristles longer; prescutellum undeveloped; subscutellum moderately large. Katepisternum with two bristles and additional setulae; anepisternum usually bare, but haired in *Periscelis annulipes* Loew; other pleural sclerites bare. Upper margin of anepimeron with two rather large pleural wing processes, the anterior one having a button-like swelling (greater ampulla) as in Calyptratae. Metasternal area usually bare, but setulose in some species of *Scutops* Coquillett.

Wing (Fig. 3) short and broad, uniformly milky in Nearctic species, variously patterned in brown in many exotic species. C without breaks or weakenings beyond humeral crossvein, ending abruptly at R_{4+5}; Sc incomplete, about half as long as R, rather sharply bent forward at end; R_1 usually bare (setose in *Neoscutops* Malloch), ending in C about middle of wing (deflected to near apex of wing in *Neoscutops*); cells bm and dm present; crossvein r-m joining cell dm at or beyond middle; crossvein dm-cu almost parallel to crossvein r-m; cell cu*p* open or closed posteriorly; A_1 not attaining wing margin. Alula large. Calypteres small; lower one undeveloped. Halter normal, whitish throughout.

Legs fairly short and stout (Fig. 1). Fore and mid femora each with a row of fairly strong posteroventral setae. Tibiae usually banded; preapical dorsal tibial bristles undeveloped. Tarsi unmodified.

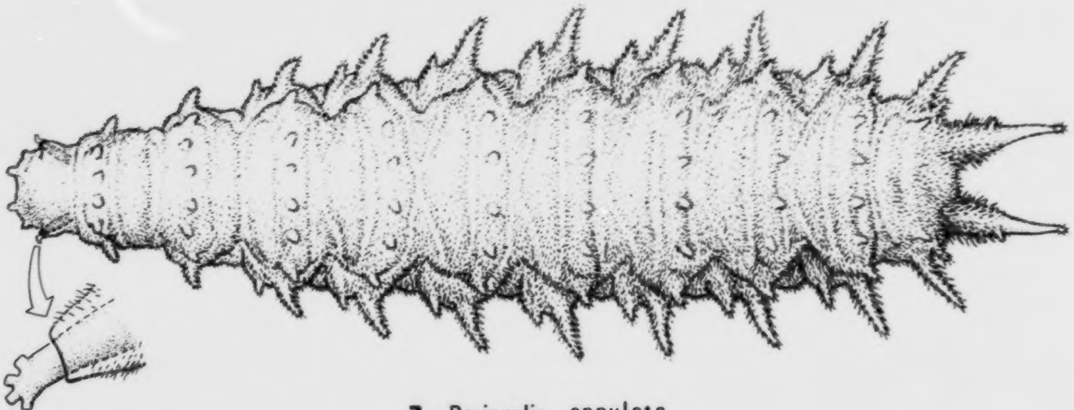
Abdomen: rather broad and dorsoventrally flattened. Male (Figs. 4, 5) with seven pairs of spiracles; first six pairs situated in membrane; seventh pair situated in pregenital sclerite (syntergosternite 7 + 8). Tergite 6 and sternite 6 well-developed, symmetric. Syntergosternite 7 + 8 large, virtually symmetric. Epandrium small and little exposed, setulose above; ventral extremity on each side produced as a surstylar lobe; base of this lobe continuous with epandrium, not articulated. Cerci fairly large, each with an elongate sclerotized anteroventrally directed lobe at apex. Hypandrium rather large, forming a bursa-like chamber; gonopod undifferentiated; paramere in form of sclerotized lobe between base of aedeagus and surstylus-like lobe of epandrium; aedeagus usually rather long and ribbon-like; aedeagal apodeme fused with hypandrium; ejaculatory apodeme large.

Female (Fig. 6) with seven pairs of spiracles. Tergite 7 and sternite 7 fused laterally, enclosing seventh spiracle. Tergite 8 and sternite 8 short and free. Ovipositor short and stout, not at all adapted for piercing. Cerci very short, free from each other. Three sclerotized spermathecae present; these smooth, spherical, with two situated on one duct and one on the other in *Periscelis annulata* (Fallén) (contrary to statement by Sturtevant 1954, p. 552).

Egg. Unusual, blackish brown in color (Sturtevant 1954).

Larva. Spiculate (Fig. 7), with conspicuous lateral and dorsal projections from all segments (Teskey 1976), somewhat as in Platypezidae, certain Sciomyzidae, Chamaemyiidae, and *Fannia* Robineau-Desvoidy. Cephalopharyngeal skeleton of standard muscomorph type, with no accessory sclerotized oral rasping surfaces. Each posterior spiracle on a long spiculate conical process arising from extreme caudal margin of terminal segment; this process differing very little in general appearance from adjacent lateral projections. Anterior spiracle (Fig. 7) small, with four short diverging digits.

Biology and behavior. The immature stages are poorly known. The adults frequent wounds and sap fluxes on trunks of deciduous trees. Larvae and adults (including teneral specimens) of *Periscelis annulata* have been collected from slime flux on bleeding elm (*Ulmus americana* L.) in Ottawa (Teskey 1976), and an adult of *P. occidentalis* Sturtevant was taken at a wound on poplar (*Populus* sp.) at Camargo in Chihuahua, Mexico. *Periscelis wheeleri* (Sturtevant) was reared from larvae in fermenting oak sap in Massachusetts (Sturtevant 1954) and also from galleries of the cerambycid *Sternochetus lapathi* (Linnaeus) on willow (*Salix* sp.) in British Columbia (Hennig 1969).



7 Periscelis annulata

Fig. 77.7. Dorsal view of the mature larva of *Periscelis annulata* (Fallén), with enlargement of the left anterior spiracle in left lateral view.

Classification and distribution. The family Periscelididae as now defined (Sturtevant 1954, 1963; Hennig 1969, 1973) is primarily Neotropical in distribution. It contains five genera: *Diopsosoma* Malloch, *Marbenia* Malloch, *Neoscutops* Malloch, *Periscelis* Loew, and *Scutops* Coquillett. Only the Holarctic genus *Periscelis*, with three extant and one extinct species, occurs in the Nearctic region. The precise phylogenetic position of the family is still obscure. Griffiths (1972) placed it (including the genus *Somatia* Schiner) in the Nothyboidea along with Nothybidae, Teratomyzidae, and Psilidae. Hennig (1973) placed it in a subgroup (Periscelidea) of the superfamily Anthomyzoidea with the Aulacigastridae, Teratomyzidae, and Asteiidae. One fossil species is known, *Periscelis annectans* Sturtevant from Mexican amber of Miocene age (Sturtevant 1963). The only comprehensive treatment of the family is by Sturtevant (1954). Hennig (1969) added new South American records.

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ASTEIIDAE

78

Curtis W. Sabrosky

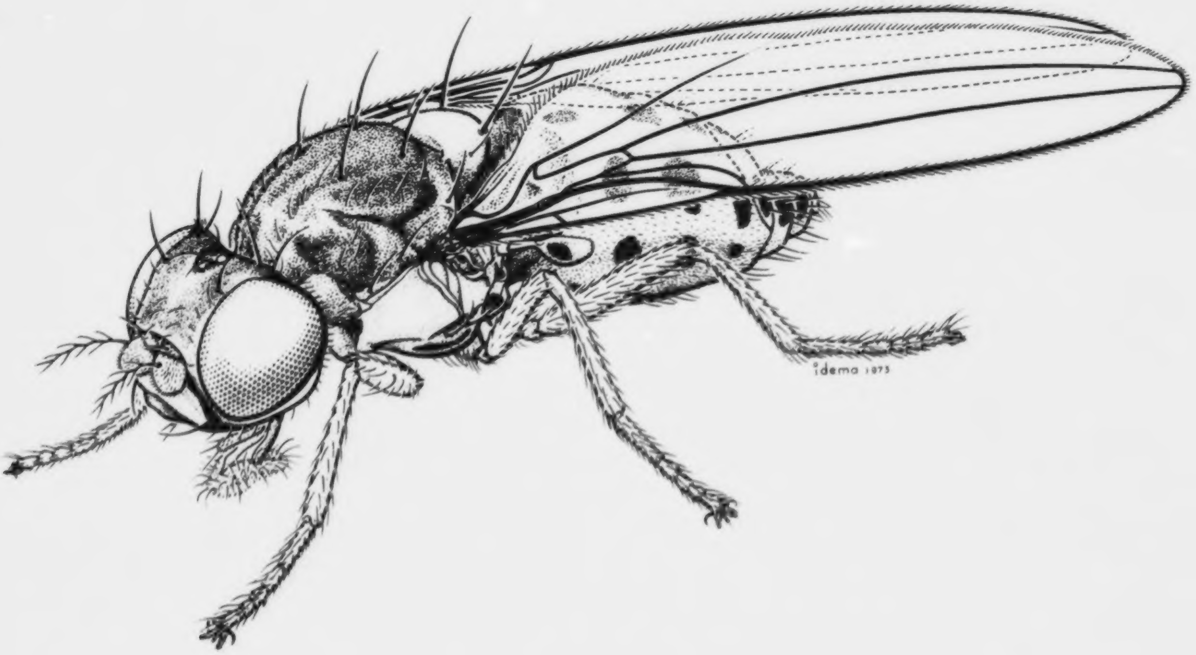


Fig. 78.1. Adult female of *Asteia beata* Aldrich.

Tiny flies (Fig. 1), 1.0–2.5 mm long. R_{2+3} usually extremely shortened and ending in C with or a little beyond R_1 (Fig. 6), except in *Leiomyza* Macquart (Fig. 7); ultimate section of M_1 forming a long anteriorly concave arc.

Adult. Head: large, higher than long (Figs. 2, 3), elongate in several exotic species, as broad as or broader than thorax, distinctly concave behind when viewed from above, and with posterior outline of head following anterior curvature of thorax. Eye bare, large, occupying most of head as seen in profile. Frons broad in both sexes, at most with scattered hairs, usually with fronto-orbital plates not demarcated from frontal vitta. Inner and outer vertical bristles usually strong; postocellar bristles minute, divergent, weak and hair-like, often difficult to discern; ocellar bristles short or hair-like, proclinate and divergent; one or two pairs of orbital bristles present; these usually reclinate, but proclinate in *Leiomyza* and absent in *Loewimyia* Sabrosky; no frontal bristles present, but frontal plate with a series of tiny reclinate setulae. Face flat or slightly concave, almost as broad as frons, usually slightly narrowed below level of antennal bases, usually broad at vibrissal level but decidedly narrowed in *Sigaloessa* Loew. Parafacial linear and gena narrow, except in exotic species. Vibrissa usually well-developed, but pale, slender, and inconspicuous. Antenna short, decumbent; arista elongate except in *Loewimyia* (Fig. 5) and in an exotic genus, sometimes bare but usually with alternating minute to long side hairs, giving arista a characteristic zigzag appearance (Figs. 1, 4). Palpus present; proboscis short and fleshy.

Thorax: disc of proepisternum rounded, not carinate; prosternum small, subquadrate, without precoxal bridge except in *Leiomyza*. Scutum convex (Fig. 1), longer than broad, sparsely haired; acrostichal hairs ranging from absent to one or two rows of fine pale inconspicuous hairs; scutellum short and broad, apically rounded, convex on disc, without hairs; postnotum large; subscutellum often well-developed and projecting. Chaetotaxy: postpronotal bristles usually absent, but these weakly present in *Astiosoma* Duda, and one to four dorsocentral bristles present in *Sigaloessa*; usually one anterior and one posterior notopleural bristle present, but no anterior one and one posterior one in some *Leiomyza* and one anterior one and two posterior ones in some Pacific species of *Asteia* Meigen; one postalar and occasionally one presutural supra-alar and one postsutural intra-alar bristle present; one to three katepisternal bristles present; anepisternum usually bare, finely haired in *Leiomyza* and *Phlebosotera* Duda, never with bristles; proepisternal, proepimeral, and anepimeral bristles and setulae absent; two pairs of marginal scutellar bristles present; basal scutellar bristles often so weak and hair-like that scutellum appears to have only one pair of bristles.

Legs short and slender (Fig. 1), without distinctive features. Tibiae without preapical dorsal bristles.

Wing (Figs. 6, 7) usually longer than body, hyaline, unspotted. C unbroken, especially strong beyond juncture of R_1, extending to M_1 at apex of wing, and with an outstanding setula near insertion of M_1. Sc present but incomplete apically; R_{2+3}, except in *Leiomyza* (Fig. 7), unusually short, abruptly curved forward to join C at or near juncture of R_1; R_{4+5} and M_1 long, convergent distally and narrowing cell r_{4+5}; ultimate sector of M_1 forming a long anteriorly concave arc; A_1 usually not attaining margin of wing except as a streak. Crossvein bm-cu absent; cells bm and dm confluent; cell dm long and narrow, open distally in *Asteia* and relatives where crossvein dm-cu absent. CuA_2 weak or absent, and consequently cell cu*p* absent, though position often marked by faint streaks or folds, most evident in *Phlebosotera* (Fig. 6).

Abdomen: narrow, mostly membranous with reduced or weakly sclerotized tergites except in *Leiomyza* (Figs. 8–11). Both sexes lacking spiracles on abdominal segment 7; spiracles 2–6 situated in margins of tergites. In male (Figs. 8, 9), surstylus more or less fused with epandrium, bilobate in *Leiomyza*, symmetric in some genera, asymmetric in *Asteia* spp., sometimes decidedly so; hypandrial arms more or less fused with sternite 10, thus firmly linked to surstyli; true hypandrial bridge absent; cercus long-haired; small parameres present; aedeagus large, heavily sclerotized distally; aedeagal apodeme rod-like; ejaculatory apodeme large. Female terminalia (Figs. 10, 11) simple, weak; cercus short, long-haired; two sclerotized spermathecae present.

Biology and behavior. Little is known of the biology of the Asteiidae. Adults have often been collected on windows or at bleeding wounds on trees; *Leiomyza* spp. have been found on fungi. A few varied rearing records from parts of the world other than the Nearctic suggest that the larvae may be scavengers, perhaps in the frass left by other insects. Adults have been reared from fungi, from stalks of *Cannabis sativa*, from debris in hollow trees, from buds of *Gossypium* infested with *Anthonomus grandis grandis* Boheman, and from dried stems of the giant reed *Phragmites australis* subsp. *australis*, along with species of *Lipara* Meigen (Chloropidae).

Classification and distribution. The family is small, with 11 genera and slightly over 100 species described in the world fauna; over half the species belong in the genus *Asteia*. Some occur in all faunal regions, and many new species should be found as these tiny and delicate flies are more thoroughly collected and studied. The world genera were keyed by Sabrosky (1956), and a synopsis of New World species was published by Sabrosky (1957). A fossil genus and species, *Succinasteia carpenteri* Hennig, is known from Baltic amber (Hennig 1969).

Key to genera

1. Crossvein dm-cu present; alula present though sometimes narrow, margined with long hairs (Figs. 6, 7) 2

Crossvein dm-cu absent; alula absent and wing margin bare in alular region 6

2. R_{2+3} long, ending in C well beyond R_1 (Fig. 7). Anepisternum with numerous fine hairs .... **Leiomyza** Macquart

4 spp.; widespread; Sabrosky 1957

R_{2+3} short, ending in C with or only slightly beyond R_1; section of C between R_1 and R_{2+3}, at most, as long as crossvein r-m (Fig. 6). Anepisternum bare except in *Phlebosotera* 3

3. Anepisternum with numerous hairs. CuA_2 and cell cu*p* clearly outlined by traces or folds in wing; cell cu*p* truncate distally (Fig. 6) .... **Phlebosotera** Duda

3 spp.; widespread; Sabrosky 1957

Anepisternum bare. CuA_2 and cell cu*p* at most weakly indicated; cell cu*p* not truncate distally 4

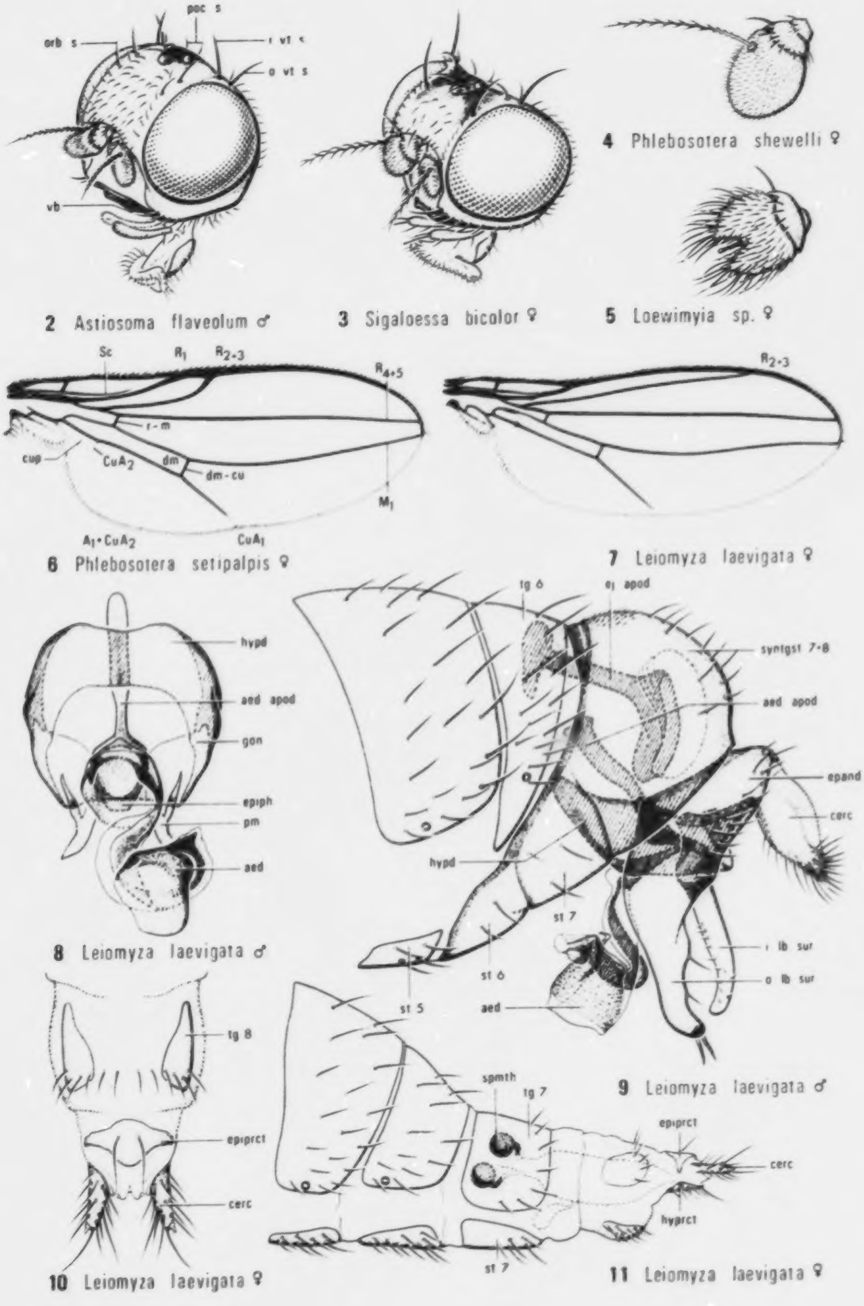
4. One pair of strong erect reclinate orbital bristles present, about midway on frons as seen in profile; inner vertical bristle absent or short and inconspicuous compared with outer vertical; face weakly to strongly narrowed between vibrissae, with facial ridges more or less converging ventrally (Fig. 3) 5

Either two pairs of weak orbital bristles present resembling slightly stronger hairs or orbital bristles not developed; inner vertical bristle strongly developed, equal to or greater than outer vertical; face not narrowed between vibrissae, with facial ridges parallel and face approximately equal to width of frons (Fig. 2) .... **Astiosoma** Duda

4 spp.; widespread; Sabrosky 1957

5. Head depressed and elongate, in profile with its length greater than its height at the vertex and at least twice its height at the base of the antennae. Eye elongate, with its greatest length 1.5 times its greatest width; long axis nearly parallel to frons. One pair of dorsocentral bristles present. Face only weakly narrowed between vibrissae .... **Bahamia** Sabrosky

1 sp., *longiceps* Sabrosky; Bahamas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2 Astiosoma flaveolum ♂

3 Sigaloessa bicolor ♀

4 Phlebosotera shewelli ♀

5 Loewimyia sp. ♀

6 Phlebosotera setipalpis ♀

7 Leiomyza laevigata ♀

8 Leiomyza laevigata ♂

9 Leiomyza laevigata ♂

10 Leiomyza laevigata ♀

11 Leiomyza laevigata ♀

Figs. 78.2–11. Details of head, wing, and terminalia: heads of (2) *Astiosoma flaveolum* (Coquillett) and (3) *Sigaloessa bicolor* Loew; right antennae of (4) *Phlebosotera shewelli* Sabrosky and (5) *Loewimyia* sp. in left lateral view; wings of (6) *Phlebosotera setipalpis* Sabrosky and (7) *Leiomyza laevigata* (Meigen); (8) hypandrium and associated parts of *L. laevigata*, ventral view; (9) entire male terminalia of *L. laevigata*, left lateral view; (10) dorsal and (11) left lateral views of ovipositor of *L. laevigata*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; i lb sur, inner lobe of surstylus; i vt s, inner vertical seta; o lb sur, outer lobe of surstylus; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; spmth, spermatheca; st, sternite; syntgst, syntergosternite; tg, tergite; vb, vibrissa.

Head not depressed and elongate, in profile as high as or higher than long. Eye large and rounded, not elongate, at most with its length slightly greater than its height (Fig. 3). Two pairs of dorsocentral bristles present. Face strongly narrowed between vibrissae; lower margin projecting almost snout-like between vibrissal angles . . . . ***Sigaloessa*** Loew
4 spp.; southeast; Sabrosky 1957

6. Arista present; frons with one pair of strong erect reclinate orbital bristles. Acrostichal hairs usually absent (Fig. 1), but present in a few Old World species . . . . ***Asteia*** Meigen
3 spp.; widespread; Sabrosky 1957

Arista inconspicuous or absent (Fig. 5); frons without strong orbital bristles. Median row of acrostichal hairs present . . . . ***Loewimyia*** Sabrosky
several spp., unnamed; Florida, Texas, Mexico

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MILICHIIDAE

79

CURTIS W. SABROSKY

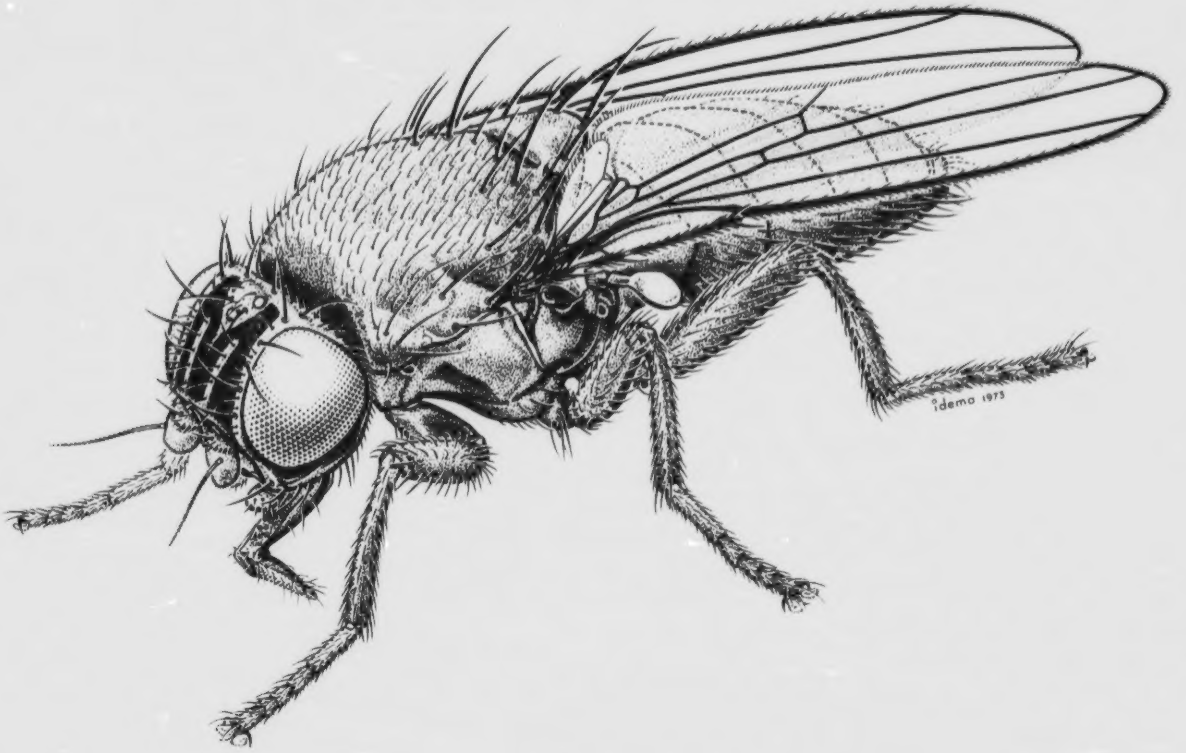


Fig. 79.1. Adult female of *Desmometopa m-nigrum* (Zetterstedt).

Small inconspicuous flies (Fig. 1), 1–5 mm long, usually black, often dull or subshining. Two or three pairs of usually lateroclinate to proclinate orbital bristles and two pairs of medioclinate frontal bristles present; frons usually with two rows of interfrontal setulae that are on distinct sclerotized strips in the commonest genus, *Desmometopa* Loew (Fig. 1). C with humeral and subcostal breaks; cell cu*p* small, closed (Figs. 12–17).

Adult. Head: higher than long, with frons in profile strongly sloping (Figs. 2–7). Eye bare, especially large in Milichiinae with linear gena (Figs. 6, 7), but smaller in Madizinae with gena usually broader (Figs. 2–5). All bristles strong; inner and outer vertical bristles present; postocellar bristles parallel or subparallel (Figs. 6, 7), or cruciate at tips (Figs. 2, 3); ocellar bristles proclinate and divergent, indistinct from hairs in *Eusiphona* Coquillett (Fig. 6). Frons broader than width of eye in both sexes of Madizinae (Figs. 2–5), but in Milichiinae sometimes narrower than width of eye (Fig. 6) and usually obviously narrower in male than in female, often emarginate anteriorly (Fig. 7), sometimes with sclerotized interfrontal strips, e.g. *Desmometopa*; two or three pairs of orbital bristles present, these usually lateroclinate, but upper ones sometimes reclinate and lowermost one sometimes proclinate; almost always with two pairs of medioclinate frontal bristles but some *Milichia* Meigen with uniform row of fine medioclinate frontal setulae on each side, and all *Eusiphona* (Fig. 6) with about 10 pairs of mostly reclinate fronto-orbital bristles, the anterior two or three pairs slightly medioclinate; lunule exposed, often extending ventrally between bases of antennae (Fig. 4); a pair of proclinate, sometimes stout, setae usually present on lunule. Face usually concave in profile; median carina low; anterior margin usually slightly projecting; antennal grooves shallow or deep; vibrissal angle distinctly angulate in Madizinae (Figs. 2–5), rounded and not angulate in Milichiinae (Figs. 6, 7); vibrissa strong; lower margin of gena with a row of subvibrissal bristles. Antenna usually short and decumbent; first flagellomere usually orbicular, but enlarged in male of *Phyllomyza* Fallén (Fig. 3) and longer than broad in *Aldrichiomyza* Hendel (Fig. 2); arista usually slender and micropubescent (Figs. 3–7), densely long-haired in *Aldrichiomyza* (Fig. 2). Palpus short in Milichiinae, commonly elongate and conspicuous in Madizinae, greatly enlarged in male of some species of *Desmometopa* and *Phyllomyza* (Fig. 3); proboscis slender, short, and rather inconspicuous to elongate and conspicuous, usually geniculate (Figs. 2–7).

Thorax: scutum convex, usually thickly and finely haired, polished or dull; scutellum bare except for marginal bristles. Proepisternum usually weakly carinate somewhat as in Chloropidae, but incompletely so in some Milichiinae; prosternum free from propleuron or joined to it by means of a precoxal bridge. Chaetotaxy: one to several postpronotal bristles and one anterior and one posterior notopleural bristle present; usually one presutural and one postsutural supra-alar, one to five dorsocentral, one or two prescutellar acrostichal, and two marginal scutellar bristles present; proepisternal bristle present, sometimes pale and weak; proepimeral bristle absent; anepisternum and anepimeron usually bare; katepisternum usually with one bristle in Madizinae, two or three in Milichiinae.

Wing (Figs. 12–17) hyaline, unspotted, with veins strong and distinct. C with humeral and subcostal breaks; in Milichiinae C usually with a deep notch at subcostal break overlapped by a costal lappet (Figs. 16, 17); C continuing to M_1 except in *Paramyia* Williston (Fig. 12) and *Aldrichiomyza*, and with short uniform black marginal setae that extend to or just beyond end of R_{2+3}. Sc usually complete, often pale and inconspicuous distally; R_{2+3} very long, ending a little before apex of wing. Cell r_{4+5} often narrowed at apex (Figs. 15, 17); cell dm long; crossvein dm-cu present except in *Paramyia* (Fig. 12); crossvein bm-cu present, separating cells bm and dm; cell cup present, closed, but very short and sometimes difficult to see, typically acute distally (Figs. 15–17), often ending in streak-like trace of A_1 (Figs. 12, 17).

Legs slender, weak, usually without distinctive features (Fig. 1). Tibiae lacking preapical dorsal bristles; hind tibia broadened and flattened in male of *Leptometopa* Becker (Fig. 18), and, in some species, with a slightly countersunk elongate oval tibial organ posterodorsally that is reminiscent of a similar feature in many Chloropidae.

Abdomen: slender in Madizinae, typically broadened and flattened in male of Milichiinae, especially in those species with tergites conspicuously silvery pruinose. Seven spiracles present in both sexes; spiracles 1–5 usually situated in membrane. Male terminalia (Figs. 10, 11) studied in detail by Hennig (1937) and Griffiths (1972), symmetric, usually with a single sclerotized pregenital complex dorsally composed of parts of segments 6–8 and bearing sixth and seventh pairs of spiracles; surstylus movable; hypandrial arms connected directly to sternite 10; true hypandrial bridge absent; gonopod and paramere reduced; aedeagus short, typically bare, with small sclerotized basiphallus and chiefly membranous distiphallus. Female terminalia (Figs. 8, 9) with cerci separate, variably developed; two slender weakly sclerotized spermathecae present (*Leptometopa* and *Pholeomyia* Bilimek) or absent; spermathecal ducts long, fine, and rolled into a single spool-like coil (Sturtevant 1925–1926).

Larva. Few described, but those known active, slender, and elongate, tapering anteriorly, subtruncate posteriorly. Anterior spiracles ranging from short with a number of short rounded papillae to elongate and branched with numerous long finger-like papillae (Fig. 19). Posterior spiracles borne on a prominent short or long spiracular stalk; spiracular stalk strongly directed outward making posterior end of body appear forked in Madizinae (Fig. 20), but cylindrical and parallel resembling those of Chloropidae and some other families in Milichiinae, and with a characteristic row of more or less conical papillae or lobes dorsal to bases in Madizinae (Fig. 20). Best descriptions and figures by Zimin (1948) (*Desmometopa*, as "*tarsalis* F."), Hennig (1956) (*Leptometopa* spp.), and Moser and Neff (1971) (*Pholeomyia comans* Sabrosky).

Puparium. Short, tapering at both ends.

Biology and behavior. Larvae of Milichiidae are saprophagous or coprophagous. They have been reared from manure, garbage, compost heaps, debris in the crotch of a tree, laboratory breeding media, bird's nests, and decaying plant material such as pomegranates, cowpea seeds, potatoes, coffee, cherries, and cacti. Some species are associated with ants, and several of these have been reared from the waste material of fungus gardens deep in the nests of leaf-cutting ants (*Atta* Fabricius). Others have been reared from the nests of *Crematogaster* Lund and *Azteca* Forel.

Adults are often taken in flowers. Some have a commensal relationship with spiders and predatory insects such as Asilidae and Reduviidae, riding on them and sucking juices that exude from their prey. Adults of some species in Africa utilize regurgitated food from ants on *Crematogaster*-infested trees.

Classification and distribution. The family consists of 19 genera and over 225 species in the world, with apparently many undescribed species. Two subfamilies, Madizinae and Milichiinae, are recognized. Twelve genera and 37 species are known in America north of Mexico. Many of the genera are virtually world wide in distribution, and some of the scavenger species have been widely disseminated in commerce. The generic key by Melander (1913), although not entirely satisfactory and including several genera not belonging to the Milichiidae, is still the most nearly complete key to the genera of the world. Two species are known as fossils, *Phyllomyza jaegeri* Hennig from Baltic amber (Hennig 1967) and *Phyllomyza hurdi* Sabrosky from Mexican amber (Sabrosky 1963).

Key to genera

1. Vibrissal angle 90° or less, with vibrissa below level of lower margin of eye (Figs. 2–5); head in profile subquadrate, usually as long as or longer than high. Wing (Figs. 12–14) without conspicuously broadened anal area; width at anal angle equal to or less than width at crossvein dm-cu; subcostal notch seldom evident, never well-developed .... MADIZINAE....2

Vibrissal angle scarcely or not at all evident; vibrissa well above lower margin of eye (Figs. 6, 7); head in profile rounded below, obviously higher than long. Wing (Figs. 15–17) with conspicuously broad anal area; width at anal angle greater than at crossvein dm-cu; subcostal notch usually evident, sometimes strongly so, with basal sector of C ending in an acute lappet .... MILICHIINAE....9

2. C extending only to R_{4+5} (Fig. 12) 3

C extending to M_1 (Figs. 13–17) 4

3. Crossvein dm-cu absent (Fig. 12). Arista slender, pubescent .... ***Paramyia*** Williston

1 sp., *nitens* (Loew); widespread

Crossvein dm-cu present. Arista thickened at base, densely long-haired (Fig. 2) .... ***Aldrichiomyza*** Hendel

1 sp., *agromyzina* (Hendel); eastern

4. Frons with three pairs of orbital bristles that are lateroclinate over eyes (Fig. 3) (not to be confused with medioclinate frontal bristles) 5

Frons with two pairs of lateroclinate orbital bristles (Figs. 4, 5) 6

5. Lower margin of head (vibrissal axis) obviously shorter than greatest length of head (antennal axis); orbital plate broad, distinctly separated from frontal plate; proboscis short; labella short and fleshy; antenna and palpus of male usually greatly enlarged or elongate (Fig. 3). Body of Nearctic species black .... ***Phyllomyza*** Fallén

3 spp.; Holarctic, 2 southeastern; Malloch 1913

Lower margin of head equal or subequal to greatest length of head; orbital and frontal plates narrow, fused; proboscis elongate, slender, and geniculate; antenna and palpus not sexually dimorphic. Body yellow, very small .... ***Stomosis*** Melander

2 spp.; 1 southeastern, 1 Neotropical and in Arizona; Sabrosky 1958

6. Frons with two rows of interfrontal setae borne on gray sclerotized interfrontal strips; strips and concolorous fronto-orbital plates and ocellar triangle demarcating a dull to velvet black M-shaped area (Fig. 1) .... ***Desmometopa*** Loew

10 spp.; widespread; Sabrosky 1983

Interfrontal setae, if present on frons, not on sclerotized strips that are concolorous with fronto-orbital plates (Figs. 4, 5) 7

7. Lunule extended ventrally on midline of face as a flat plate between antennae, reaching nearly to lower margin of face; lower margin of face usually extended dorsally, subtriangular (Fig. 4). Anepimeron with short stout bristle. Hind tibia of male greatly broadened (Fig. 18) .... ***Leptometopa*** Becker

2 spp.; widespread

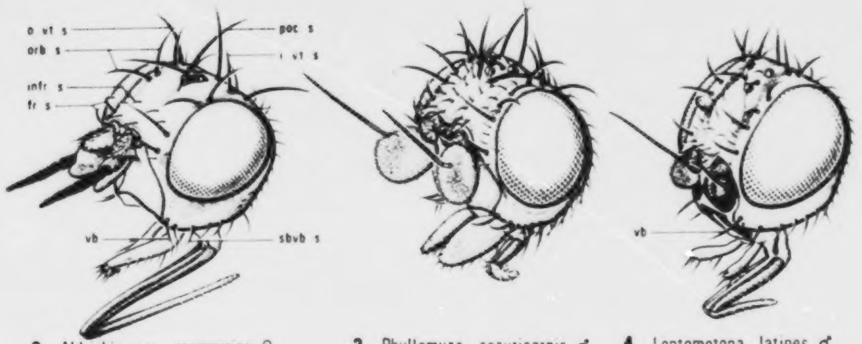
Lunule not extended ventrally on midline of face as a flat plate dividing antennae (Fig. 5). Anepimeron bare. Hind tibia not enlarged in male 8

8. Body polished black. Frons much longer than broad (Fig. 5). Cell dm long; crossvein dm-cu almost equidistant from wing margin (along CuA_1) and from crossvein r-m (Fig. 13) .... ***Madiza*** Fallén

2 spp.; widespread

Body dull black or subshining; thorax finely dark gray pruinose. Frons short, broader than long. Cell dm short; crossvein dm-cu two or three times as far from wing margin as from crossvein r-m (Fig. 14) .... ***Neophyllomyza*** Melander

2 spp.; 1 widespread, 1 western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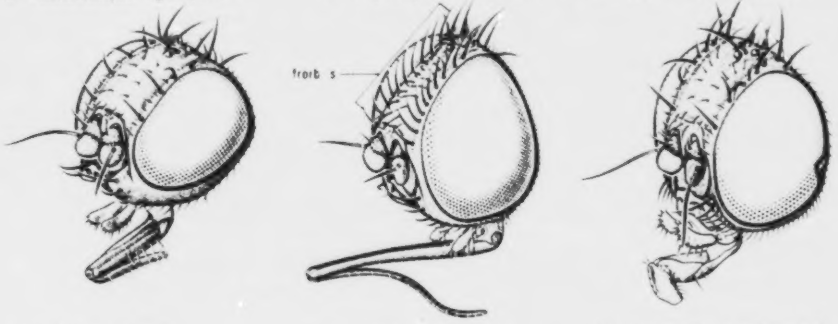
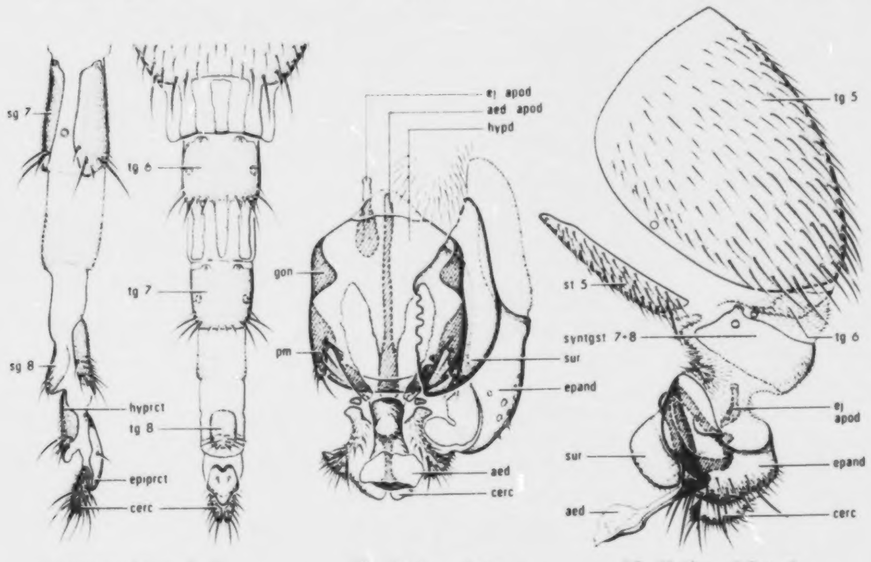
2 Aldrichiomyza agromyzina ♀ **3** Phyllomyza securicornis ♂ **4** Leptometopa latipes ♂



5 Madiza glabra ♂ **6** Eusiphona mira ♀ **7** Milichiella lacteipennis ♀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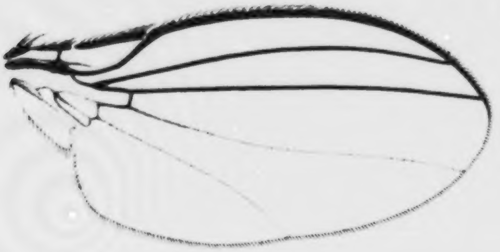
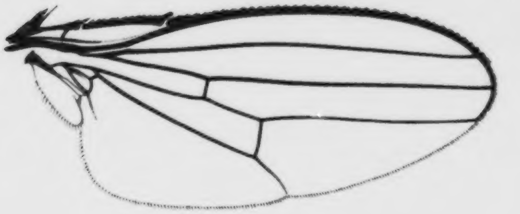
8 Madiza glabra ♀ **9** **10** Madiza glabra ♂ **11** Madiza glabra ♂

Figs. 79.2–11. Heads and terminalia: heads of (2) *Aldrichiomyza agromyzina* (Hendel), (3) *Phyllomyza securicornis* Fallén, (4) *Leptometopa latipes* (Meigen), (5) *Madiza glabra* Fallén, (6) *Eusiphona mira* Coquillett, and (7) *Milichiella lacteipennis* (Loew); (8) left lateral and (9) dorsal views of female terminalia of *Madiza glabra*; (10) hypandrium and associated parts of *Madiza glabra*, ventral view; (11) male terminalia of *Madiza glabra*, left lateral view.

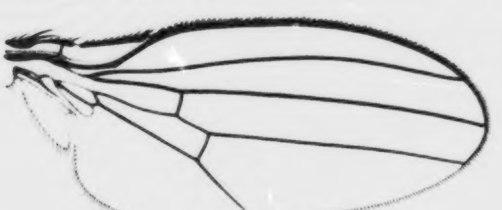
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; frorb s, fronto-orbital seta; fr s, frontal seta; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; infr s, interfrontal seta; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; sbvb s, subvibrissal seta; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; vb, vibrissa.



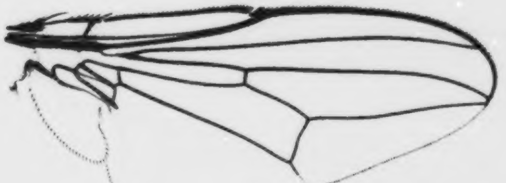
12 Paramyia nitens ♀



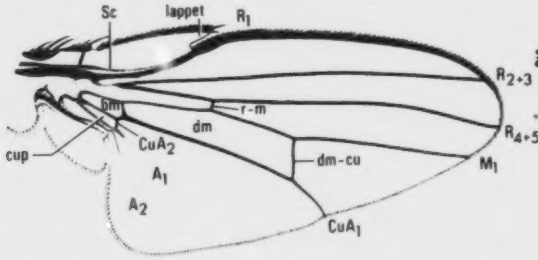
13 Madiza glabra ♂



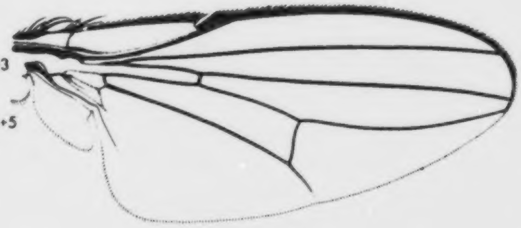
14 Neophyllomyza quadricornis ♀



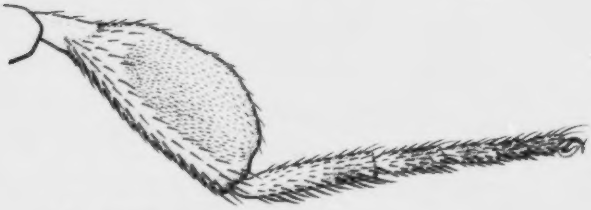
15 Eusiphona mira ♂



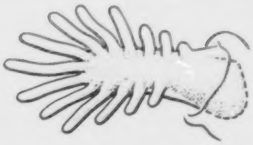
16 Pholeomyia indecora ♂



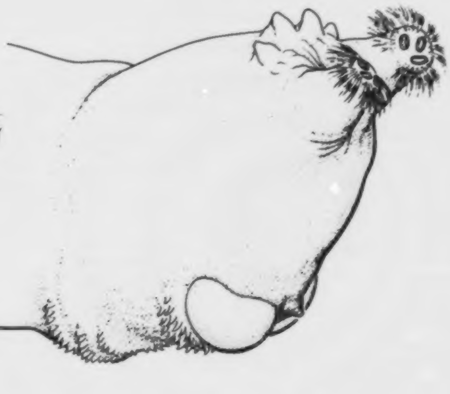
17 Milichiella lacteipennis ♀



18 Leptometopa latipes ♂



19 Desmometopa m-nigrum



20 Desmometopa m-nigrum

Figs. 79.12–20. Wings, legs, and larvae: wings of (12) *Paramyia nitens* (Loew), (13) *Madiza glabra* Fallén, (14) *Neophyllomyza quadricornis* Melander, (15) *Eusiphona mira* Coquillett, (16) *Pholeomyia indecora* (Loew), and (17) *Milichiella lacteipennis* (Loew); (18) left hind tibia of male of *Leptometopa latipes* (Meigen), anterior view; (19) anterior spiracle of larva of *Desmometopa m-nigrum* (Zetterstedt); (20) posterior spiracles of larva of *D. m-nigrum*.

9. Frons with eight to ten pairs of uniformly arranged fronto-orbital bristles, all erect and reclinate, showing no distinction between orbital and frontal series (Fig. 6); ocellar bristles short, weak, and hair-like. Proboscis strongly geniculate, exceptionally long and slender (Fig. 6), except in an undescribed species .... ***Eusiphona*** Coquillett

3 spp.; widespread; Sabrosky 1955

Frons with two or three pairs of orbital bristles and two pairs of frontal bristles; foremost pair of orbitals proclinate or nearly so; uppermost pair of orbitals reclinate; both pairs of frontals medioclinate (Fig. 7); ocellar bristles strong. Proboscis weakly geniculate, short with fleshy labella (Fig. 7) 10

10. Anepisternum posteriorly with row of strong bristles .... ***Pholeomyia*** Bilimek

12 spp.; widespread; Sabrosky 1959, 1961

Anepisternum bare 11

11. Posterior margin of eye notched (Fig. 7) .... ***Milichiella*** Giglio-Tos

5 spp.; widespread; Melander 1913

Posterior margin of eye entire .... ***Milichia*** Meigen

1 sp., *aethiops* Malloch; southwestern

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CARNIDAE

80

Curtis W. Sabrosky

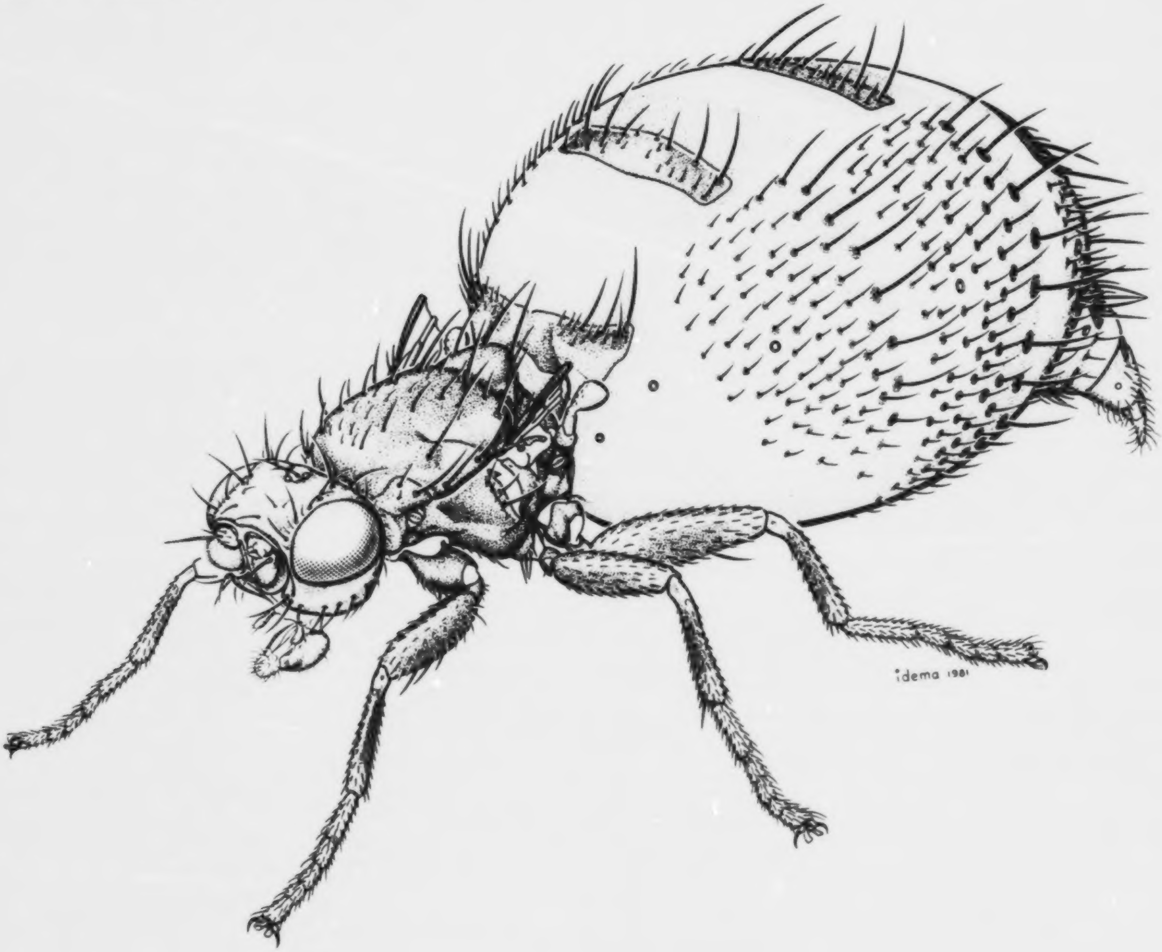


Fig. 80.1. Dealated adult female of *Carnus hemapterus* Nitzsch.

Small more or less shining black flies (Fig. 1), 1–3 mm long, with two upper pairs of lateroclinate orbital bristles and two lower pairs of medioclinate frontal bristles (Fig. 4). Prementum short and bulbous, followed by short and rather inconspicuous labella. C with both humeral and subcostal breaks. Anepisternum with one or more bristles.

Adult. Head: bristles well-developed (Fig. 4), including two upper pairs of lateroclinate orbital and two lower pairs of medioclinate frontal bristles; vibrissae strong, each followed by a row of strong subvibrissal bristles; frons usually without rows of interfrontal setae, rarely with more than one anterior supra-antennal pair of cruciate interfrontal bristles and a few fine hairs near apex of ocellar triangle; postocellar bristles short, usually parallel or slightly diverging, cruciate in two species of *Meoneura* Rondani. Antenna often in a deep antennal groove. Prementum usually broad, thick, and bulbous, followed by short rounded relatively inconspicuous labella.

Thorax: one strong postpronotal, one presutural and one postsutural supra-alar, two notopleural, one to four dorsocentral, and two pairs of scutellar bristles present; anepisternum usually with hairs and one or more bristles; anepimeron usually bare; propleuron bare. Prosternum a median sclerotized area, without precoxal bridge.

Legs slender (Fig. 1), without distinctive features. All tibiae without preapical dorsal bristle.

Wing (Figs. 2, 3) hyaline, usually broken off some distance from base in *Carnus* Nitzsch. C with both humeral and subcostal breaks; subcostal break distinct but without costal lappet or deep notch; C extending to R_{4+5} in *Carnus* (Fig. 3) and *Meoneura*, and to M_1 in *Hemeromyia* Coquillett (Fig. 2); Sc complete, although faint and weak distally; R_{2+3} typically bisinuate; ultimate section of M_1 and A_1 only weakly indicated and cell cu*p* not closed in *Carnus* and *Meoneura*, but veins strong and cell cu*p* closed in *Hemeromyia*.

Abdomen: normally developed except in *Carnus*, in which tergites and sternites are greatly reduced (Fig. 1); sternites absent and abdomen typically inflated with its membrane beset with numerous setiferous sclerotized spots in female of this genus.

Male terminalia (Figs. 7, 8) with tergites 6–8 fused and asymmetric, sometimes greatly reduced or absent; spiracles of segment 6 situated in or near membrane, except in *Carnus*; those of segment 7 present or absent. Surstylus articulated, movable, sometimes bifid, sometimes spectacularly developed (*Meoneura*); hypoproct sometimes with lateral lobes bearing tufts of long hairs (*Meoneura*); cercus small, poorly differentiated. Hypandrium bearing small gonopods and parameres; aedeagus long, flexible, partly coiled when retracted, distally with abundant short felt-like hairs or pubescence.

Female terminalia (Figs. 5, 6) with cerci fused into a single stylus-like structure that is acute or narrowly rounded apically; two sclerotized spermathecae present, or absent (*Meoneura*).

Larva. Few species known, and none described in detail. Larva typical of Muscomorpha, slender, narrowly tapering anteriorly, broad posteriorly.

Puparium. Blunt at each end; two slender tubular divergent spiracular stalks present posteriorly, apical in *Carnus* but decidedly preapical in *Meoneura*, each ending in three short curved finger-like projections (de Meijere 1912, Hennig 1937); each projection presumably bearing a spiracular opening (not specifically noted in available descriptions or figures).

Biology and behavior. Except for the avian associate of *Carnus hemapterus* Nitzsch, species of this family are saprophagous and are associated with carrion or excrement. Many have been reared from bird's nests. Adults of *Carnus* are generally assumed to be bloodsucking, but some workers believe that they feed on excretions of the skin. Both larvae and adults are found in bird's nests, and the adults are often seen on nestling birds. Bequaert (1942) assembled much information on *Carnus hemapterus*, and Guigan *et al.* (1983) reviewed what is known on its distribution and biology.

Classification and distribution. This small family, chiefly Holarctic, contains slightly more than 40 described species, most of them in the genus *Meoneura*. The group has commonly been treated as a subfamily of Milichiidae, but recently it has been classified as a distinct family and has even been placed in a different superfamily from that of the Milichiidae. Hennig (1972) and Griffiths (1972) have discussed the relationships of the Carnidae, and Hennig (1972) presented a key to the world genera. One fossil species, *Meoneurites enigmatica* Hennig, is known from Baltic amber (Hennig 1972).

Key to genera

1. Wing usually broken off, leaving a short stub (Fig. 1); if wing complete (Fig. 2), crossvein dm-cu absent. Female with abdominal sternites 1–5 absent; membrane with numerous setiferous sclerotized spots . . . . **Carnus** Nitzsch

1 sp., *hemapterus* Nitzsch; Holarctic, southern Canada to Mexico; Bequaert 1942

Wing complete; posterior crossvein dm-cu present. Female with all abdominal sternites present; membrane at most sparsely bristled 2

2. Cell dm long; crossveins r-m and dm-cu widely separated. C extending to M_1; M_1 distinct. Cell cu*p* closed; A_1 strong (Fig. 2) . . . . ***Hemeromyia*** Coquillett

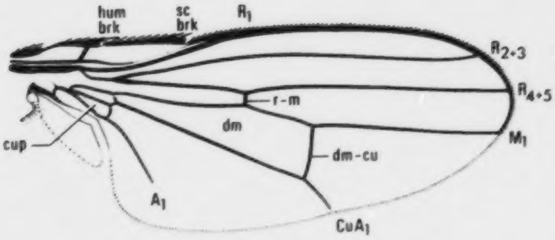
2 spp.; western

Cell dm short; crossveins r-m and dm-cu narrowly separated. C ending at R_{4+5}. Cell cu*p* open; A_1 weak, streak-like . . . . ***Meoneura*** Rondani

13 spp.; widespread; Sabrosky 1959, 1961

Figs. 80.2–8. Wings, head, and terminalia: wings of (2) *Hemeromyia* sp. and (3) *Carnus hemapterus* Nitzsch; (4) head of *C. hemapterus*; (5) ventral and (6) dorsal views of female terminalia of *Meoneura obscurella* (Fallén); (7) ventral and (8) left lateral views of male terminalia of *M. obscurella*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; fr s, frontal seta; gon, gonopod; hum brk, humeral break; hypd, hypandrium; hyprct, hypoproct; i vt s, inner vertical seta; lbl, labella; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; premnt, prementum; proc, process; sbvb s, subvibrissal seta; sc brk, subcostal break; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; vb, vibrissa.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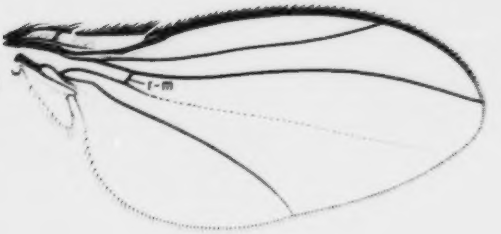
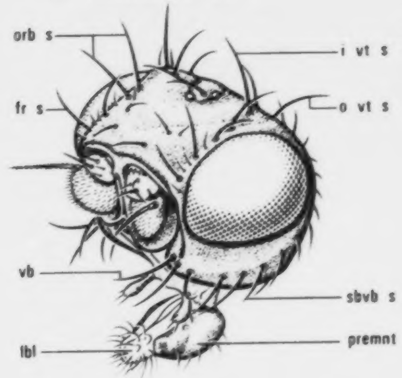
2 Hemeromyia sp. ♂



3 Carnus hemapterus ♀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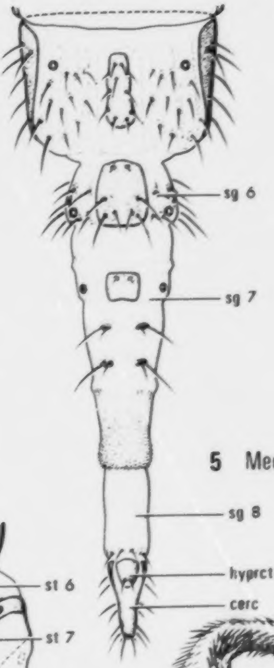
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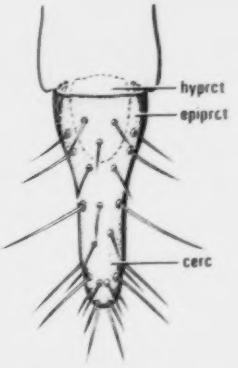
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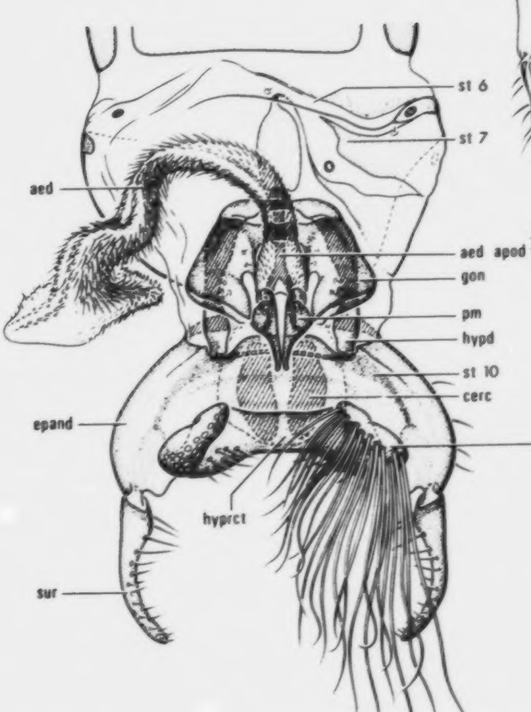
5 Meoneura obscurella ♀ **6**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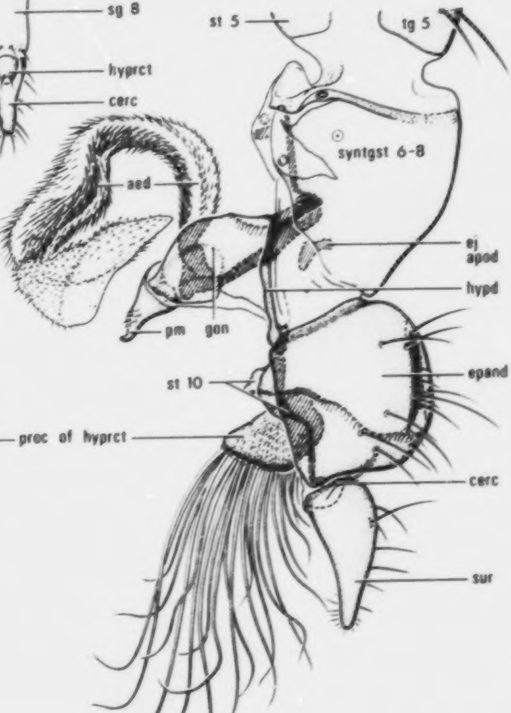
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7 Meoneura obscurella ♂

8 Meoneura obscurella ♂

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BRAULIDAE

81

B. V. Peterson

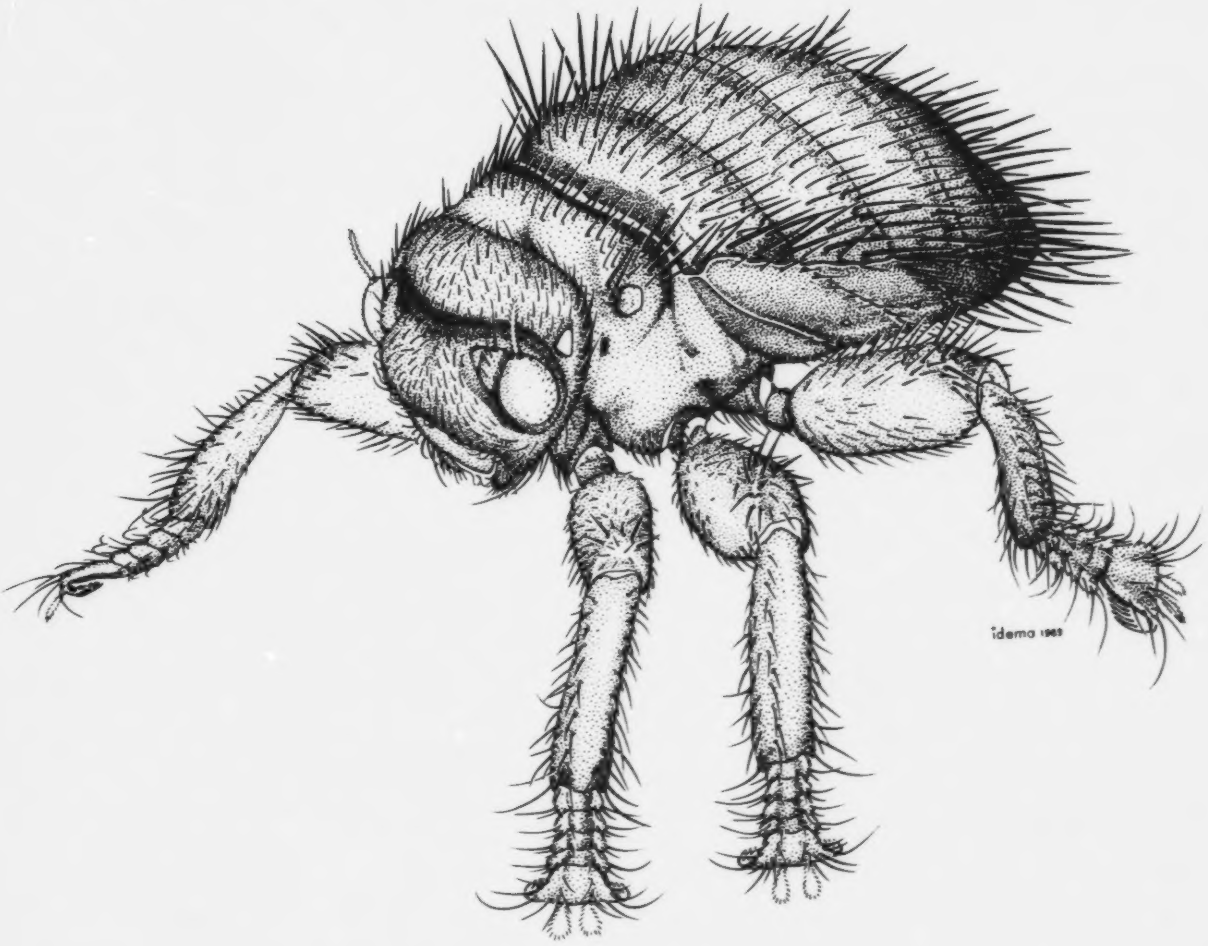


Fig. 81.1. Female of *Braula coeca* Nitzsch.

Small flies, convex, ovoid and heavily sclerotized, without wings, halteres, and scutellum (Fig. 1); length ranging from about 1.5 to 1.7 mm. Head short; eyespots minute and without ocelli. Claws modified, comb-like. Abdomen with six pleural sclerites; body covered generally with numerous stiff setae and bristles. Immature stages live in wax combs of honey bees and adults attach themselves to adult honey bees.

Adult. Head: short, compressed from front to back (Fig. 1), slightly wider than thorax but narrower than abdomen, vertically oriented and somewhat triangular in shape; posteroventral area concave and shaped to accomodate fore coxae. Frons short and broad, with numerous short stiff setae and about six longer stout bristles lateral to eyespot; ptilinal fissure very distinct and open above bases of antennae, with an internal wedge-shaped sclerotization medially. Eyespot minute, pale, weakly developed, and often difficult to see; ocelli absent. Face broad, slightly convex, with numerous fine stiff setae; frontogenal suture weak but usually discernible. Gena narrow, bearing several stout bristles. Bases of antennae broadly separated; each antenna short, lying in a deep antennal pit from which it projects laterally; scape very small, hidden in the pit; pedicel larger, subglobose to somewhat tear-drop in shape, with one long stout dorsal seta and several more slender setae ventrally; first flagellomere somewhat larger than pedicel, subglobose to somewhat reniform in shape, covered with numerous sensory setulae, and bearing a single-segmented arista bearing short setulae. Frontoclypeal suture distinct. Clypeus moderately large, in the form of a flattened subtriangular bare plate. Proboscis short; labrum small but distinct; clypeolabral suture and membrane distinct but withdrawn in dried specimens; labrum surrounded laterally and ventrally by labella that project as two short slender setose lobes; prementum about as long as labella, moderately sclerotized, with a pair of moderately long stiff setae anteroventrally; palpus single segmented, rather large, flattened, and somewhat crescent-shaped, slender proximally, broad and rounded distally, with long marginal setae.

Thorax: consisting of a single short convex mesonotal plate (Fig. 1) fused anteroventrally with elements of postpronotum; "antepronotum vestigial remaining merely as a rim to the cervical concavity" (Speight 1969); postpronotal lobes not developed; scutellum absent; postnotum greatly reduced and withdrawn, represented dorsally by a very narrow transverse membranous area having a weakly sclerotized anterior margin (mediotergite); membranous laterotergal area widening ventrally to level of tiny posterior spiracle and bearing a series of very small sensory sensilla. Propleural suture faint but discernible in cleared specimens; prosternum and proepisternum united by a precoxal bridge; two tiny faintly sclerotized plate-like sclerites present anterior to precoxal bridge, perhaps representing lateral cervical plates. Anterior spiracle large, situated high on anepisternum, circular in shape, often visible in dorsal view as a crescent-like indentation; mesopleuron with only a faint indication of being divided into anepisternal and katepisternal areas by an anapleural suture; epimeron reduced, only faintly indicated. Posterior half of dorsum of thorax covered by short setae and with a row of moderately long stiff setae on hind margin, with two or three longer stouter bristles at posterolateral corners and usually two similar bristles just in front of anterior spiracle. Wing, calypteres, and halter absent.

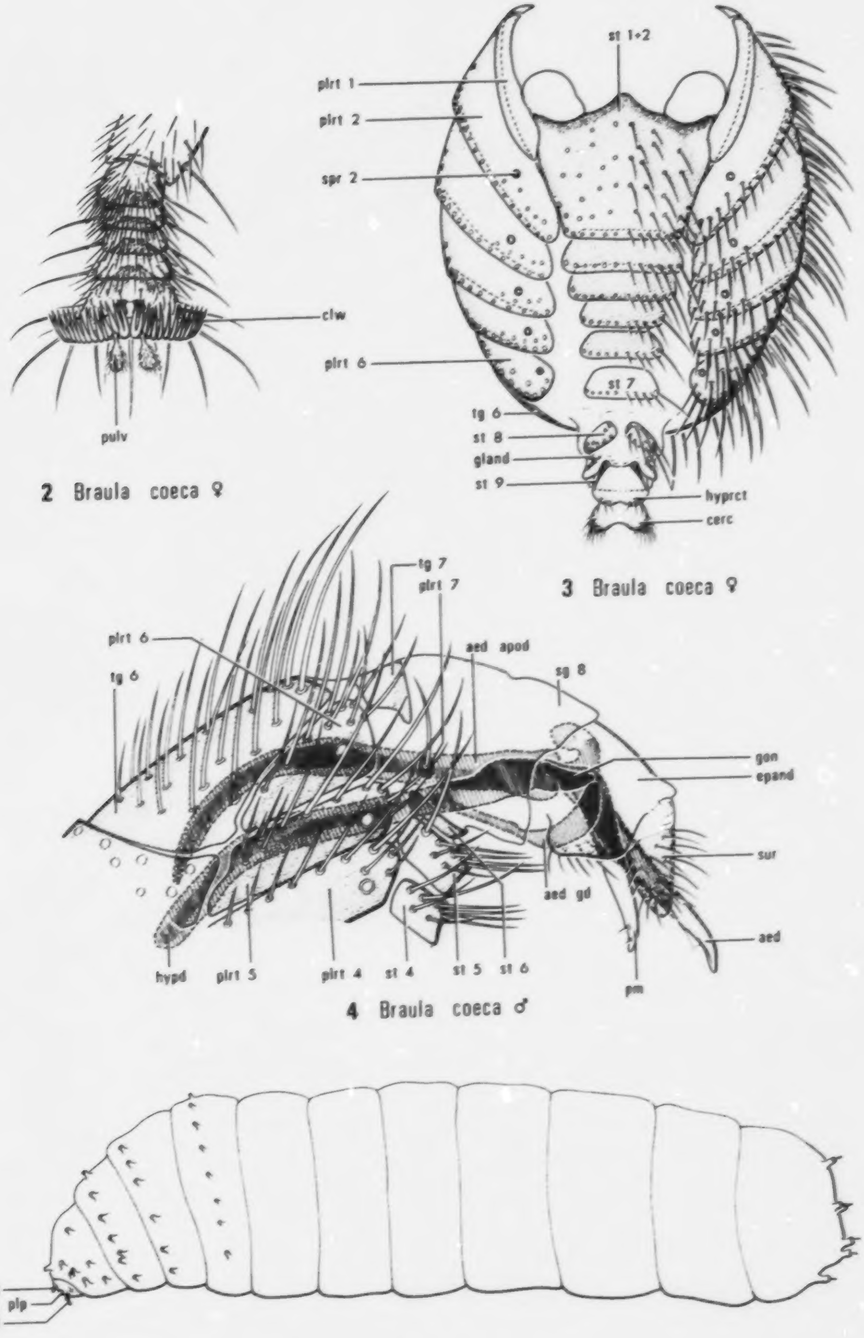
Legs (Fig. 1) rather stout, subequal in length but relatively long in proportion to body size, with moderately dense long and short setae. Femora with setae mostly confined to dorsal half of anterior surface but including a patch of longer stouter bristles apically on dorsal surface; posterior surface of femora bare; a series of rather long setae present on both anteroventral and posteroventral margins. Coxae broadly separated; anterior coxa largest; other coxae much smaller. Proximal four tarsomeres of each leg uniformly short (Fig. 2), subquadrate; apical tarsomere enlarged, triangular in shape; all tarsomeres with several long pale setae; claws (Fig. 2) modified as comb-like structures composed of about 12–16 retrorse teeth; claws of each leg separated at midline; pulvilli clavate, short and pale but conspicuous, setose apically; empodia absent.

Abdomen: short, broad, strongly convex, somewhat ovoid in outline, broadly attached to thorax (Fig. 1); both sexes with five visible tergites (syntergite 1 + 2 and tergites 3–6); remaining segments usually withdrawn. Pleural area of abdomen with heavily sclerotized pleurites that are separated from tergites dorsally by pale narrow sutures and extend ventrally almost to sternites, perhaps representing lateral extensions of tergites or secondary sclerotizations arising in pleural membrane; pleurites 1 and 2 are situated ventral to syntergite 1 + 2; pleurites 3–6 decreasing in size posteriorly; pleurites of segments 2–6 enclosing spiracles 2–6; true spiracle 1 probably lost; female with a very small gland-like opening in membrane on each side just posterior and dorsal to plates of sternite 8. Five visible sternites present in both female and male when abdomen not extended, but sternite 6 small and obscured in male; synsternite 1 + 2 large, as long as or slightly longer than combined lengths of remaining sternites, essentially pentagonal in shape, pointed anteriorly, with hind margin straight; remaining sternites rectangular, decreasing in width posteriorly. Hind margins of tergites, pleurites, and sternites with long stiff setae; tergites with scattered short discal setae and a group of several stouter and longer bristles near lateral margins; pleurites usually without discal setae or with only a very few; synsternite 1 + 2 with discal setae; discal setae absent on remaining sternites.

Female (Fig. 3) with segment 7 onwards, when at rest, withdrawn into segment 6; dorsally these segments largely membranous; sternite 7 slightly smaller and more weakly sclerotized than sternite 6, bearing a row of marginal setae posteriorly; sternite 8 present as two small separate sclerites each bearing a few discal and marginal setae; sternite 9 represented by a tiny lateral subtriangular plate internally on each side and associated with a slender longitudinally oriented bar-like sclerite that articulates with hypoproct; epiproct tiny, faintly sclerotized, connected ventrally with a larger faintly sclerotized setose plate-like hypoproct. Cerci small but distinct, fused medially but with a posteromedian emargination; each lobe rounded and setose. A single small spermatheca present, associated with a pair of small accessory glands (Alfonsus and Braun 1931).

Male (Fig. 4) also with terminal segments, when not in use, withdrawn into segment 6; tergite 7 rectangular, wider than long, weakly sclerotized, occasionally with a lateral bristle situated on a small sclerotized base that possibly represents a remnant of pleurite 7; sternite 7 fused with syntergosternite 8. Syntergosternite 8 wider and longer than tergite 7, mostly membranous but weakly and narrowly sclerotized basally. Epandrium convex and bare dorsally, but with a few setae along margin ventrally; surstylus short but distinct, subtriangular with short setae; cerci tiny, fused, subtriangular. Sternite 10 present as two small sclerotized plates. Ventral sclerites between sternite 6 and hypandrium absent. Hypandrium a rather stout Y-shaped structure subequal in length to long aedeagal apodeme, open posteriorly; hypandrial bridge absent; a small triangular gonopod situated at apex of each arm of hypandrium and separated from it by a fine but distinct suture; a lightly sclerotized aedeagal guide present, situated between arms of hypandrium and extending posterodorsally where it articulates ventrally with base of aedeagus and extending anterodorsally to ventral margin of aedeagal apodeme; aedeagal apodeme unusually long, rod-like, free from hypandrium; aedeagus a simple, sclerotized, tapering tubular structure with a ventral membrane; ejaculatory apodeme absent; paramere well-developed, slender, digitiform, slightly shorter than aedeagus, bearing a few sensory setulae ventrally near apex.

Egg. Moderately large in relation to size of female, ranging from about 0.63 to 0.81 mm in length and 0.28 to 0.34 mm in diameter; shape oval but one side somewhat less convex; surface finely pitted, surrounded by two lateral ir-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2 Braula coeca ♀

3 Braula coeca ♀

4 Braula coeca ♂

5 Braula coeca

Figs. 81.2–5. *Braula coeca* Nitzsch: (2) mid tarsus of female, ventral view; (3) abdomen and terminalia of female, ventral view; (4) male terminalia, lateral view; (5) larva.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; ant, antenna; cerc, cercus; clw, claw; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; md, mandible; mx plp, maxillary palpus; plrt, pleurite; pm, paramere; pulv, pulvillus; sg, segment; spr, spiracle; st, sternite; sur, surstylus; tg, tergite.

regular and coarsely reticulate exochorionic flanges that apparently serve as a flotation device to prevent newly hatched larva from drowning in liquid honey.

Larva. Somewhat cylindrical in shape, tapering anteriorly, rounded posteriorly, about 2.25 mm long, with three distinct thoracic and eight abdominal segments. Respiratory system metapneustic.

Cephalic segment somewhat bilobate, with small but distinct peg-like antennae and with small maxillary rudiments bearing tiny palpi; four pairs of small sensory organs present, one pair between antennae, two pairs on maxillary organs, and one pair situated laterally between antennae and maxillae. Cephalic segment also with a characteristic sclerotized band posteriorly that some authors suggest might represent a vestige of a head capsule. Cephalopharyngeal skeleton consisting of a pair of simple stout curved mandibles, each with a posterodorsal process, fused hypopharyngeal and tentoropharyngeal sclerites, and an annular labial sclerite that is incomplete dorsally; dorsal and ventral cornua elongate, without ridges or grooves, but with a small ventral process anteriorly.

Thoracic segments and abdominal segments 1 and 8 with characteristic girdles or bands of tubular sensory processes; prothorax with two bands and other segments with a single band of these sensory processes; those on abdominal segment 8 more diffuse in orientation; dorsalmost process longest, others decreasing in size ventrally and sometimes spine-like; these organs on anterior body segments with a toothed distal margin whereas those on abdominal segment 8 have a smooth distal margin with a central projecting seta. Posterior spiracles very small and inconspicuous, each with three oval openings.

The larva of *Braula coeca* Nitzsch (Fig. 5) has been described and figured by Skaife (1922), Arnhart (1923*a*), Hennig (1938*a*, 1952), Imms (1942), and Hassanein and Abd El-Salam (1962*a*). The preceding description is modified largely from that of Imms (1942).

Pupa. Without a true puparium but enclosed within unmodified skin of third-stage larva, pale in color, devoid of sclerotization, and not in the usual barrel-like shape. Cephalic segment and anterior two thoracic segments forming a knob-like protrusion anteriorly, giving pupa a subtriangular or pear-shaped form. Length ranging from about 1.4 to 1.7 mm.

Biology and behavior. Important contributions to the biology and behavior of Braulidae have been made by a number of authors including Skaife (1922), Arnhart (1923*a*, 1923*b*), Phillips (1925), Argo (1926), Suire (1931), Örösi Pal (1938), Hennig (1938*a*), Imms (1942), Kaschef (1959), and Hassanein and Abd El-Salam (1962*b*). Recent biological studies on *Braula coeca* infesting colonies of bees in the state of Maryland have been made by Smith (1978). The following summary is drawn in part, with permission, from the observations of Dr. I. B. Smith (personal communication).

Braula coeca overwinters in the hive as adults. The female begins to lay eggs in May, with oviposition continuing throughout the summer and fall. The eggs are laid on the undersides of the caps of the honey cells just before they are sealed by the bees. Newly emerged larvae bore tunnels into the undersides of the caps where they apparently feed on honey, pollen grains, and organic debris found in the wax. The larvae move with ease in these tunnels, which are enlarged as the larvae grow. Before pupating in these tunnels, the larvae cut fine circular grooves on the inner walls (Herrod-Hempsall 1931). Twenty-one days from the time of oviposition the adults emerge. The emerging adult forces open the circular weakened area of the tunnel wall with its inflated ptilinum and crawls out through the hole. The newly emerged adult is pale white and requires about 12–16 hours to turn to its normal reddish brown color. Shortly after emerging, the adult seeks out an adult bee to which it attaches itself by its unique comb-like tarsal claws (Fig. 2). This claw is well suited for firmly grasping the branched hairs of the host, a necessary adaptation for living on rapidly moving and flying honey bees (Phillips 1925). A honey bee normally harbors one, or occasionally two braulids. However, a queen bee may harbor as many as 30 or more braulids at one time, especially between mid-June and the end of October. Queen bees may be favored by braulids over other castes partly because of the pheromones produced by the queens or the specialized diet they are fed. Braulid adults feed on drops of liquid (presumably honey or partly so) taken from the mouthparts of the bees.

Braula coeca is generally regarded as an inquiline in bee hives. They certainly are not beneficial to the hive, but the extent of the damage they cause remains unknown. The feeding activity of the adults probably does not affect the bees much but their form of attachment and their activities may cause some irritation. The larval tunnels in comb honey, however, limit its sales value. *Braula* seems to infest weak colonies of bees and especially those that are not properly housed or cared for (Phillips 1925). Colonies become infested initially through the swarming activities of honey bees, the drifting of infested bees from colony to colony, during raids on weak colonies by bees from strong colonies, and by mechanical transport of infested combs to other hives.

Classification and distribution. The aberrant and specialized structure of *Braula* Nitzsch has long kept its taxonomic position in controversy. In describing the genus and species, Nitzsch (1818) allied it with the Pupipara, as did Müggenburg (1892), Massonnat (1909), Hendel (1928), and Brues and Melander (1932 and later editions). Skaife (1922) showed that *Braula* laid eggs and thus was not pupiparous but oviparous. However, as early as 1858, Leuckart had demonstrated differences between the female reproductive organs of *B. coeca* and those of truly pupiparous flies. Müggenburg (1892) mentioned that Leuckart believed that he had occasionally found eggs of *Braula* in the cells of honey combs, and Müggenburg himself had never found larvae inside the female. Other authors related *Braula* to the Phoridae (Borner 1908, Bezzi 1916, Séguy 1924, Handlirsch 1925). Schmitz (1917) placed *Braula* in the Acalyptratae near the Sphaeroceridae. Hendel (1936–1937), diverging from his paper of 1928, grouped them with the Agromyzidae, Coelopidae, and Odiniidae, and Imms (1942) placed *Braula* near the Chamaemyiidae. Hennig (1938*b*) related them to an assemblage of families including the Asteiidae, Periscelidae, Mormotomyiidae, and Chloropidae plus others that he later grouped in his superfamilies Milichioidea and Drosophiloidea. In 1958, Hennig placed the family Braulidae in the Milichioidea, and in 1973 he put them in a group of unplaced families. Speight (1969) suggested that *Braula* occupied an isolated position in the Acalyptratae or perhaps could be placed in the Drosophiloidea. Griffiths (1972) said the closest relatives of the Braulidae could be sought in the superfamilies Lonchaeoidea and Lauxanioidea, or if it did not belong there, Braulidae should be referred to a separate monobasic superfamily. Rohdendorf (1974) relegated Braulidae to its own infraorder, the Braulomorpha. In the present work the Braulidae is considered to be an isolated specialized family possibly allied to the family Carnidae. Further study in light of our expanding knowledge of the acalyptrate families should help to clarify its true position among these families.

The family is widespread, with members occurring in most major continental areas of the world except in the Oriental region. In North America it has been reported in many of the eastern states extending as far west as Alabama in the south, Ohio, and Wisconsin in the north. McAlpine (1979) reported it in southern Canada but I am unable to verify this report.

Many authors such as Stone (1965, 1966) consider there to be but a single species, *Braula coeca*, in the family. On the other hand, Örösi Pal (1966) described, illustrated, and keyed five species and two subspecies in the world fauna. Clearly, the family needs a thorough study on a world basis to adequately resolve the number of valid species. There appears to be only one species, *B. coeca*, in the Nearctic region. No fossils are known.

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COELOPIDAE

82

J. R. VOCKEROTH

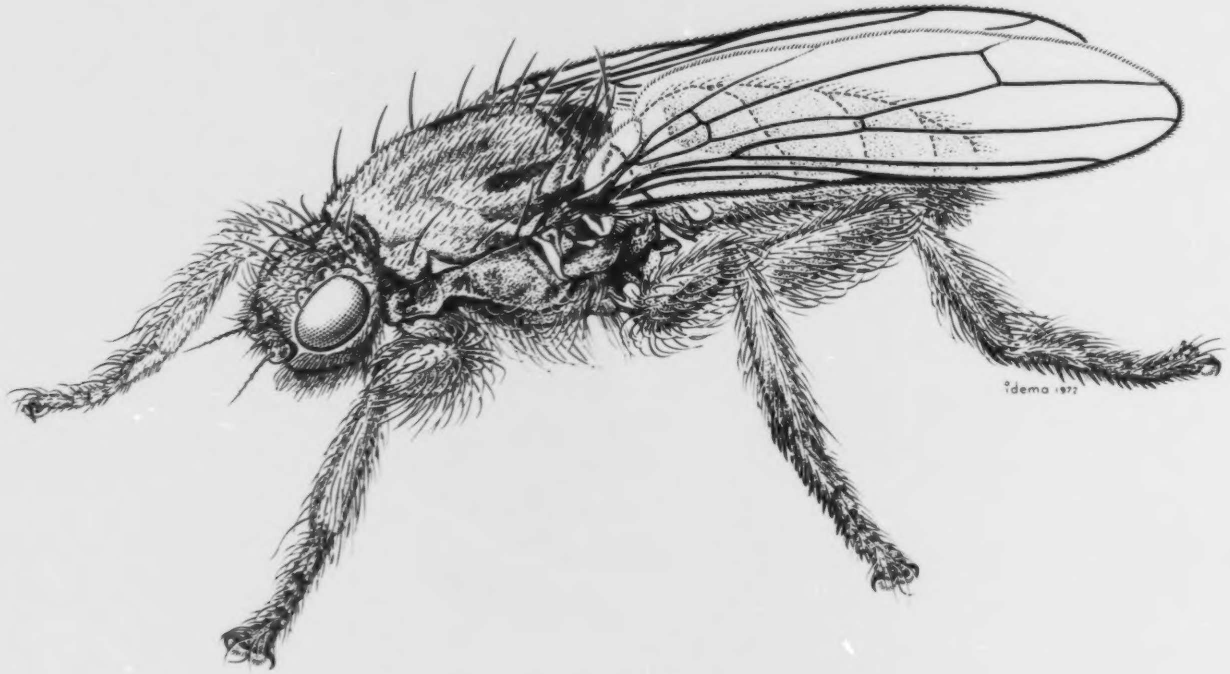


Fig. 82.1. Adult male of *Coelopa stejnegeri* Aldrich.

Robust flies (Fig. 1), 3.7–8.9 mm long, black or grayish black, shining to subshining, depressed, with a slightly to strongly flattened thoracic dorsum. Wing unmarked, fully developed in Nearctic species, slightly to markedly reduced in two subantarctic species.

Adult. Head: face in profile strongly concave (Fig. 3), uniformly sclerotized; facial ridges slightly to strongly convergent below. Gena from one-half to three-quarters height of eye; clypeus well-developed, narrowly to broadly exposed medially, laterally partly or entirely hidden in subcranial cavity. Eye oblique. Frons parallel-sided or very slightly broadened anteriorly; fronto-orbital plate narrow, extending entire length of frons; frontal vitta broad, strongly sclerotized. Chaetotaxy: two upper frontal bristles present, outcurved, with few to many interspersed hairs that extend onto parafacial; one or two anterior hairs sometimes bristle-like, but lower frontal bristles not definitely present; few to many hairs of variable length and strength on frontal vitta, with one or more pairs sometimes bristle-like; one pair ocellar bristles present, reclinate, long or very short; inner vertical bristle long; outer vertical bristle long or very short; postocellar bristles long or short, parallel to convergent; genal hairs covering at least lower three-quarters of gena, sparse to abundant, long, weak, or strong, usually with one or two anterior hairs stronger and vibrissa-like but sometimes with all hairs bristle-like. Antenna very short, appressed to face; scape with a few dorsal hairs or setae; pedicel with many dorsal and lateral hairs and setae, and with one very long dorsal subapical seta; first flagellomere not longer than pedicel, rounded apically; arista long, slender, tapering, subequal in length to least width of frons, bare or sparsely pubescent. Palpus long, stout, with few to many hairs or setae, usually with a long apical hair or bristle.

Thorax: postpronotum and scutum usually densely covered with many fine or setose hairs; only notopleuron mostly bare; in *Coelopina* Malloch hairs much sparser. Postpronotum with one or two bristles. Propleuron ventrally with one or a few hairs, weak bristles, or short setulae; prosternum narrow posteriorly, slightly to strongly broadened anteriorly, with many long strong hairs, distinctly separated from propleuron by a membranous area.

Scutum usually with two notopleural, one supra-alar, and two post-alar bristles; prescutellar dorsocentral bristle long and distinct; preceding dorsocentral bristles very short, variable in number; in male of some species postpronotal, anterior notopleural, supra-alar, inner postalar, and prescutellar dorsocentral bristles very short and stout; acrostichal hairs arranged in about 20 dense irregular rows in *Coelopa* Meigen, and in three irregular rows with distinct interspaces in *Coelopina*, with one prescutellar pair usually longer and stronger. Scutellum flat, with short hairs on margin or on most or all of disc, with two apical bristles and usually two subbasal marginal bristles; subbasal bristles, especially in male, sometimes very short. Anepimeron long, usually with a bristle and sometimes also with a few hairs or short setulae in stigmatic area, otherwise either bare or with hairs and one or several bristles on posterior half. Katepisternum with many hairs and short setae on posterior two-thirds, with one to three posterodorsal bristles, and sometimes with several long bristle-like anterior hairs. Anepimeron usually and katepimeron always bare. Laterotergite rather strongly protruding. Metepisternum with about 8–20 fine hairs or short stout setae. Metepimeron bare. Metasternal area with a very narrow bare transverse anterior portion and a well-developed detached diamond-shaped bare or haired posterior portion.

Wing (Fig. 2) with C entire and without obvious spines; Sc strong and complete, ending well before apex of R_1, but with area between their apices sometimes partly sclerotized; cell cu*p* large, somewhat angulate apically; $A_1 + CuA_2$ extending to wing margin; veins usually bare but upper and lower surface of stem of R and upper surface of apical third of R_1 sometimes setose. Wing blade posterior to cell dm frequently folded under and closely appressed to ventral surface of anterior portion (Fig. 2).

Legs with fore femur strongly swollen (Fig. 4), and with other femora moderately swollen. Femora, tibiae, and sometimes coxae with many bristles or hairs or both; hairs, when present, sometimes very long and dense. Tibiae with long dorsal preapical bristle; fore tibia without apical bristles; mid tibia with several apical bristles; hind tibia with one or a few apical and sometimes preapical bristles. Leg bristles of female and of male of smaller species usually only moderately strong, whereas those of male of larger species are sometimes extremely strong and numerous. Tarsomere 1 of fore tarsus of male with apicoventral claw-like process as wide as the tarsomere itself (Fig. 4); tarsomere 1 of hind tarsus of male with similar but narrower process; tarsomere 1 of mid and hind tarsi, and sometimes tarsomere 1 of fore tarsus and other tarsomeres, with a varying number of short spinose anteroventral and posteroventral setae.

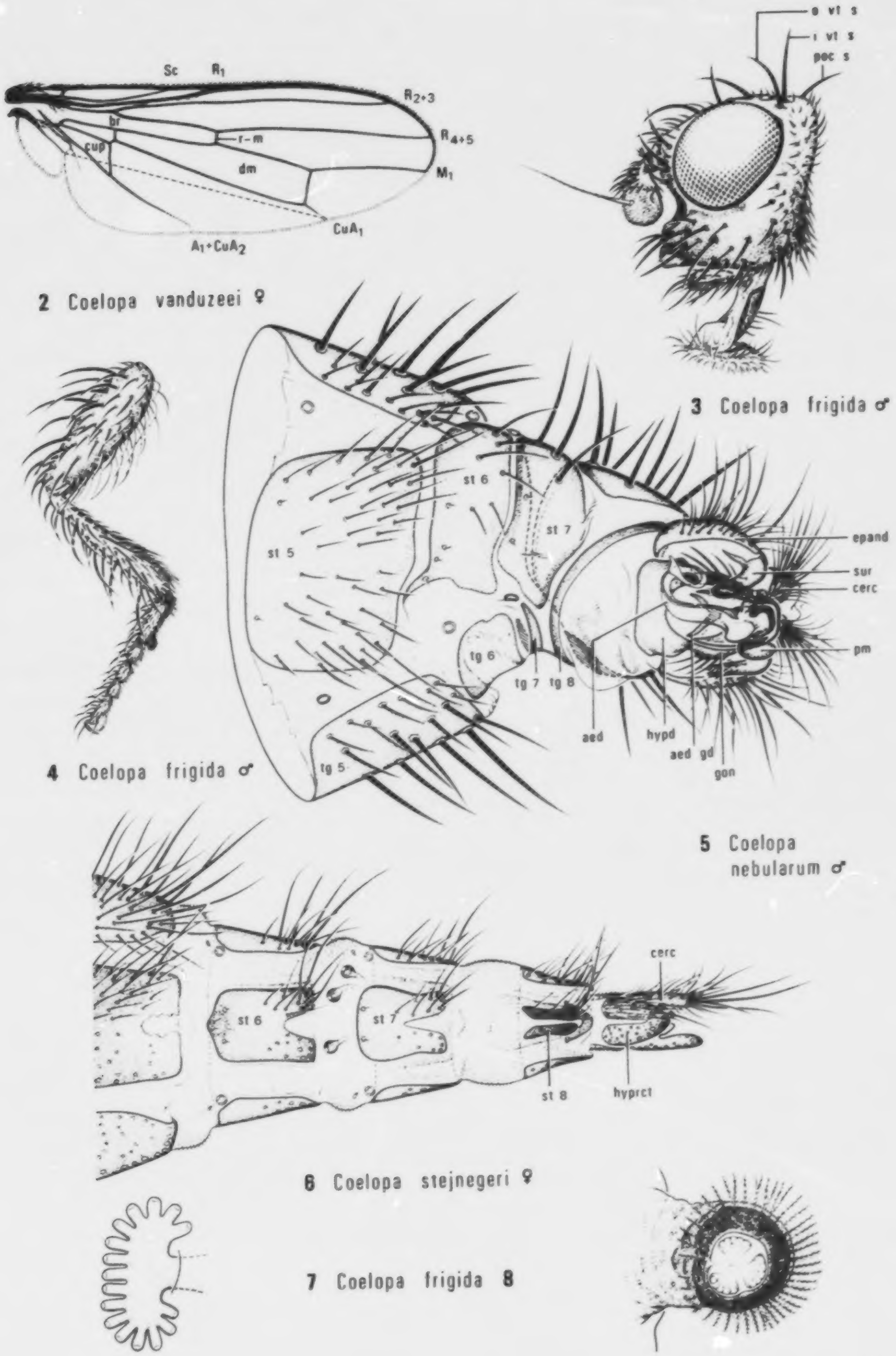
Abdomen: depressed, with tergites and sternites having vestiture varying from fine short or long hairs to strong setulae or bristles. Tergite 1 large, dorsally as long as tergite 2; sternite 1 very short, bare or with a very few hairs, partly or entirely membranous medially.

Male (Fig. 5) with sternite 5 symmetric or nearly so; posterior margin straight or very slightly and broadly emarginate. Sternites 6–8 well-developed, curving up left side of abdomen; sternite 8 large, dorsomedial in position, but slightly asymmetric; sternites 6 and 7 bare or with a few hairs; sternite 8 densely haired. Tergite 6 very short, asymmetric, bare, irregularly sclerotized, extending well down right side of abdomen where it is at least slightly broadened; tergite 7 weakly sclerotized, bare, forming a short bar or a moderately large subrectangular plate, ventrolateral in position, on right side of abdomen; tergite 8 strongly sclerotized, bare, forming a very short broad slightly asymmetric bar that is nearly midventral in position. Epandrium symmetric, twisted slightly to right when extended caudally, without process from anteroventral angle; surstylus simple, undivided, subcylindrical or slightly flattened, sometimes with apex curved forward. Hypandrium in form of a slightly flattened cylinder with ventral surface sclerotized only anteriorly and dorsal surface weakly sclerotized; gonopod fused with hypandrium, represented by a slightly projecting setose lobe or by one or a few setae on ventrolateral surface of sternite; paramere absent in *Coelopa*, present as a rather large flattened weakly sclerotized bare lobe in *Coelopina*; aedeagus complex, without epiphallus, in *Coelopa* with a pair of flattened lateral lobes near base and a slender weak filamentous apical portion, in *Coelopina* with base more swollen but without lobes and with apical third composed of two slender twisted sclerotized filaments joined by membrane; aedeagal apodeme long and slender, strongly broadened at posterior end or on posterior half, at midlength with a very weak to rather strong ventral process that has a membranous but firm connection with ventral surface of hypandrium; ejaculatory apodeme moderately large. Cerci small, weak, distinct, separate. Spiracles 1–5 located in membrane below tergites; spiracles 6 and 7 of right side located in membrane just below corresponding tergites; spiracle 6 of left side situated in membrane above left end of sternite 6, dorsolateral in position; spiracle 7 of left side situated in left end of sternite 7 slightly to left of middorsal line.

Female with segments of terminalia (Fig. 6) not strongly sclerotized, all separate with moderately long intersegmental membranes; sternite 8 divided medially in *Coelopa*, undivided in *Coelopina*. Epiproct, hypoproct, and cerci weak but distinct. Three spermathecae present, very small, widely separated, subspherical or somewhat depressed. Spiracles distinct; at least spiracles 4 and 5 situated in margins of tergites, sometimes spiracles 3–6 or 3–7 in tergites.

Larva. Typical of saprophagous Muscomorpha, namely elongate, tapering anteriorly, and subtruncate posteriorly. Surface smooth except for several rows of small spines ventrally near segmental margins. Cephalopharyngeal skeleton without peculiarities; mandibles in form of simple hooks; pharynx with filter apparatus; oral region thickly clothed with tooth-like or comb-like denticles. Anterior spiracles each with 14–18 rounded openings in a single fan-like row (Fig. 7). Terminal segment without processes surrounding spiracles; posterior spiracles each on a short separate subcylindrical process (Fig. 8); spiracular slits long, slender, curved in a semicircle; each spiracular disc with an almost complete circle of plumose hairs just inside margin (after Hennig 1937).

Biology and behavior. Species of Coelopidae are found on seacoasts, although when adults are extremely abundant they may occur far inland. The few known larvae live in rotting seaweed, which they ingest (Backlund 1945). Remmert (1959) described what appear to be two morphologically indistinguishable but biologically distinct species grouped under the name *Coelopa frigida* (Fabricius) in the North Sea area. Egglishaw (1960) discussed the biology of two British species.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2 Coelopa vanduzeei ♀
3 Coelopa frigida ♂
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4 Coelopa frigida ♂
5 Coelopa nebularum ♂
cerc
st 6
st 7
st 8
hyprct
6 Coelopa stejnegeri ♀
7 Coelopa frigida 8

Figs. 82.2-8. Details of *Coelopa* spp.: (2) wing of *C. vanduzeei* Cresson; (3) head of *C. frigida* (Fabricius); (4) foreleg of *C. frigida*; (5) male terminalia of *C. nebularum* Aldrich; (6) female terminalia of *C. stejnegeri* Aldrich; (7) anterior and (8) posterior larval spiracles of *C. frigida*.

Abbreviations: aed, aedeagus; aed gd, aedeagal guide; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; i vt s, inner verticle seta; o vt s, outer verticle seta; pm, paramere; poc s, postocellar seta; st, sternite; sur, surstylus; tg, tergite.

Classification and distribution. The family includes only about 30 described species, several of which may be synonymous. Nine described genera are recognized. *Coelopa* occurs in the Holarctic and Ethiopian regions and in Micronesia; *Coelopina* is southwestern Nearctic; *Malacomyia* Haliday is western Palaearctic; the other six genera occur only in Australia and in New Zealand and the islands to its south. The exotic species show few striking differences from the Nearctic ones. The most notable are the moderate reduction of wings in *Baeopterus* Lamb; very great reduction of wings and moderate reduction of halteres and scutellum in one species of *Icaridion* Lamb; presence of hairs or setulae on the anepimeron of three genera; absence of prosternal hairs in an undescribed genus from New Zealand; and a broadly forked surstylus in several genera.

The larval description above is based on one Palaearctic and one Holarctic species of *Coelopa*. One species of *Coelopella* Malloch and one species of *Icaridion* are the only others whose larvae have been described (Hardy 1962); *Icaridion* was referred by Hardy (1962) to *Coelopa* (*Fucomyia* Haliday). They show no significant differences from the larvae of *Coelopa* except that the anterior spiracle of *Icaridion* has the form of a strong swelling with about 10 slender filaments at each end.

The abundance and strength of bristles on the body and legs, especially in the male, varies greatly within some species. Hennig has discussed this variability in connection with *Coelopa frigida*, where the number and strength of bristles is correlated with body size. This variation has resulted in confused taxonomy at the specific level. Important specific treatments are those of Malloch (1933) (world fauna), Hennig (1937) (Palaearctic), Harrison (1959) (New Zealand), and Hardy (1962) (Macquarie Island).

The definition, limits, and relationships of the family have also been confused. Several littoral genera previously placed in the family are now referred elsewhere. There is now substantial, although not complete, agreement that the family forms a monophyletic group with the Dryomyzidae, but the relationships of this group with the Sciomyzidae *sens. lat.* are still unclear (Hennig 1937, 1958, 1965, 1971; McAlpine 1963; Griffiths 1972).

Key to genera

1. Anepimeron bare on posterior half; metasternal area haired . . . . ***Coelopa*** Meigen
4 spp.; Atlantic and Pacific coasts; Aldrich 1929

Anepimeron with many hairs and bristles on posterior half; metasternal area bare . . . . ***Coelopina*** Malloch
1 sp., *anomala* (Cole); coasts of southern California and of Baja California, Mexico

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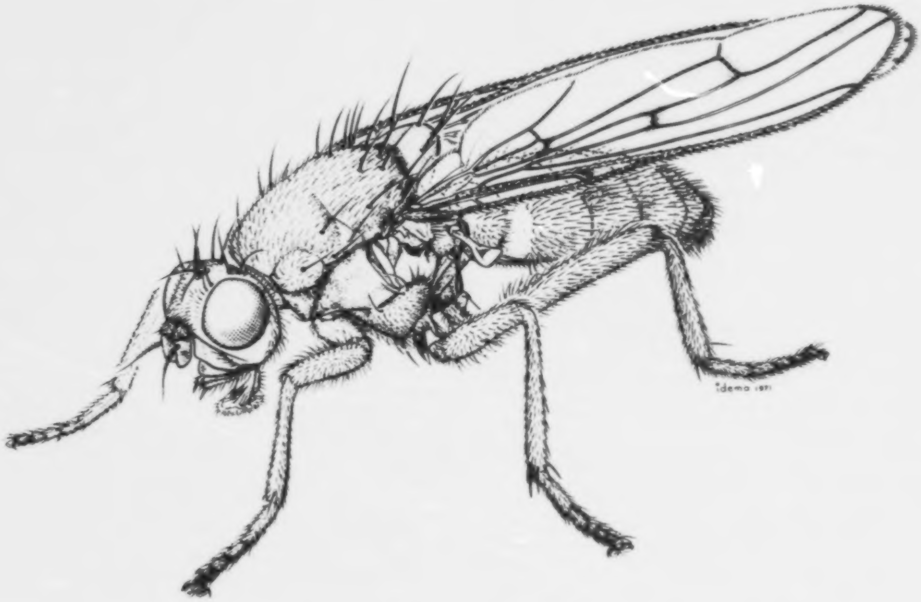
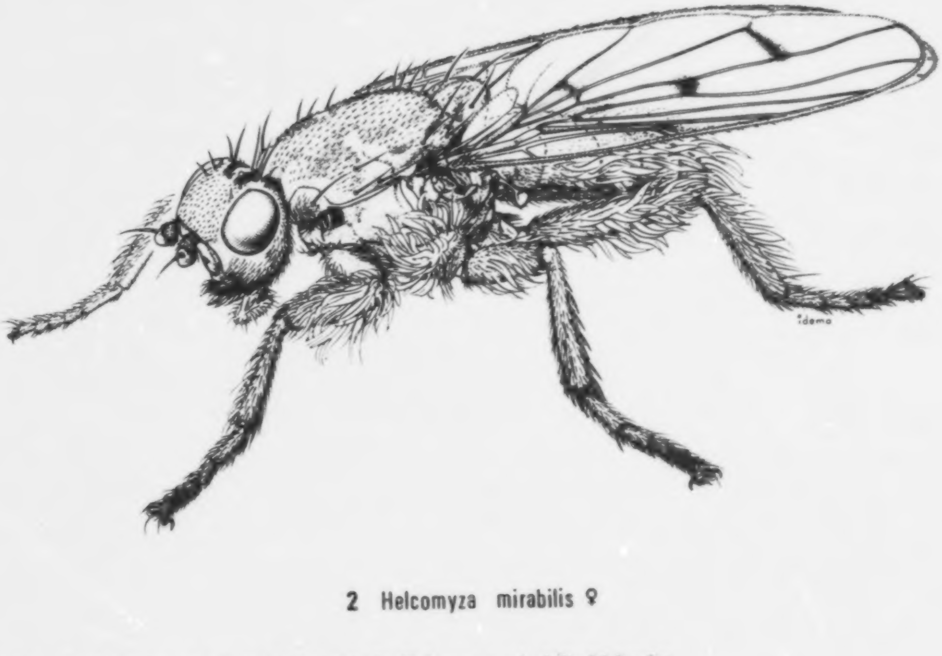
DRYOMYZIDAE

83

George C. Steyskal



1 Dryomyza anilis ♂



2 Helcomyza mirabilis ♀

Figs. 83.1–2. Adult of (1) *Dryomyza anilis* Fallén and (2) *Helcomyza mirabilis* Melander.

Medium-sized to large flies (Figs. 1, 2), moderately bristly to quite hairy, and yellowish, brown, or dark gray in color. North American species 4–12 mm in body length; some exotic species larger than 12 mm.

Adult. Head: roundish, with eye moderately large, and with gena at least one-third height of eye. Antenna of moderate size; scape and pedicel small; first flagellomere circular to elongate oval, with a subbasal bare to plumose arista. Clypeus conspicuous, sometimes protruding. Palpus and proboscis well-developed, but neither very large nor long. Chaetotaxy: no vibrissae; one inner and one outer vertical bristle present; one to several upper fronto-orbital bristles present, more or less curved outwardly over eye; one ocellar and one postocellar bristle present, the latter varying from slightly convergent to decidedly divergent.

Thorax: robust, somewhat longer than wide. Prosternum narrow and isolated (Fig. 4), or triangular and connected with propleuron (Fig. 6). Posterior spiracle roundish, fringed, without setae. Chaetotaxy: one proepisternal bristle, zero to four proepimeral bristles, usually several dorsal katepisternal bristles (in *Oedoparena* Curran with only long fine hairs), zero anepisternal, one postpronotal, and one presutural intra-alar bristle, one or two notopleural bristles, one supra-alar, two postalar, and zero or one postsutural intra-alar bristles, and one to six dorsocentral, zero or one acrostichal, and two or three scutellar bristles present. Legs slender to rather robust; preapical dorsal tibial setae present, as well as others sometimes on mid tibia; male of several species with apicoventral projection on first tarsomere of fore and hind tarsi. Wing (Figs. 3, 5) hyaline to smoky or tawny, sometimes with dark brown spots on crossvein r-m and posterior crossvein; C unbroken; Sc complete to C at some distance proximal to tip of R_1; cell cu*p* never much shorter than cell bm; crossvein bm-cu always present; CuA_2 straight or somewhat recurved; A_1 attaining wing margin, at least faintly; wing considerably reduced in one subantarctic species.

Abdomen: ovoid, often subparallel-sided in male, sometimes quite densely hairy, especially in male. Male terminalia (Fig. 7) with tergite 6 and sometimes tergite 7 small but distinct; surstylus furcate or simple, connected to posterior margin of epandrium; long projection simulating a surstylus sometimes inflected from anterior margin of epandrium; hypandrium with broad flattened lateral areas, and with one pair of gonopods and parameres; aedeagus rather short and simple, or somewhat complex and sometimes haired; base of aedeagus with more or less developed epiphallus; aedeagal apodeme long, free from hypandrium laterally; sperm pump with large ejaculatory apodeme. Female terminalia (Fig. 8) with tergites 6–8 and sternites 6–8 separate and fairly unmodified in *Dryomyza* Fallén; sternite 8 reduced or medially divided in *Helcomyza* Curtis, *Heterocheila* Rondani, and *Oedoparena*; cerci separate; two spermathecae (one plus one) in *Helcomyza* and *Heterocheila*, and three (two plus one) in *Dryomyza* and *Oedoparena*.

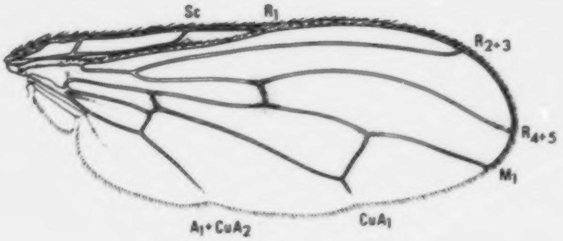
Larva. That of *Dryomyza anilis* Fallén similar to those of certain Anthomyiidae, with bilobate anterior spiracle having 18–20 marginal papillae, without lateral abdominal tubercles, with three acute lobes on each side of spiracular plate, and with three divergent spiracular openings on each round spiracular plate (Smith 1980). That of *Oedoparena glauca* (Coquillett) with similar anterior spiracle having 14 papillae, with two pairs of large fleshy lateral protuberances on each abdominal segment, and with three pairs of large rounded fleshy tubercles laterally and one pair of pointed tubercles posteriorly between spiracles on the terminal segment (Burger *et al.* 1980). Larva of *Heterocheila buccata* (Fallén) described by Backlund (1945) as bearing posterior spiracles similar to those of *Dryomyza*, but larva of *Helcomyza ustulata* Curtis described by Egglishaw (1960) as having three short oval spiracular openings in a spiracular plate bearing a long horn-like dorsal projection; neither having any cuticular lobes on terminal segment, but both having anterior spiracles with a curved row of about 10 papillae.

Biology and behavior. Species of *Dryomyza* have been reared from decaying organic matter, including carrion, decaying fungi, and dung (Burger *et al.* 1980, Smith 1980). *Oedoparena glauca* is a predator of barnacles (Burger *et al.* 1980). Helcomyzinae were reared from seaweed (wrack beds) (Backlund 1945, Egglishaw 1960).

Classification and distribution. The two subfamilies here recognized, Dryomyzinae and Helcomyzinae, were recently considered as distinct families (Steyskal 1957, 1958). Malloch (1933) first ranked the Helcomyzinae as a separate family, based chiefly upon the presence of a precoxal bridge, although he stated that the group was not in his opinion entitled to full family rank. Griffiths (1972), however, again combined the Dryomyzidae and Helcomyzidae. That course is followed here, with the two groups given subfamilial rank, as was done by Czerny (1930) in his monograph of the Palaearctic species.

Dryomyzinae, with two genera and about 20 species, are restricted to the Holarctic region. *Dryomyza* is very widespread and common; *Oedoparena* occurs only on Pacific coasts. Helcomyzinae have four genera and about 10 species, all restricted to marine coasts. Two are Holarctic, each with one Nearctic and one Palaearctic species. *Paractora* Bigot has four species in extreme southern South America and possibly one on Macquarie Island; *Maorimyia* Tonnoir & Malloch has one species in New Zealand. The Neotropical genus *Sciogriphoneura* Malloch was transferred from the Dryomyzidae to the Helosciomyzidae by Barnes (1981).

Two fossil species in Baltic amber are known, *Palaeotimia l'hoesti* Meunier and *Prodryomyza electrica* Hennig (Hennig 1965, 1969).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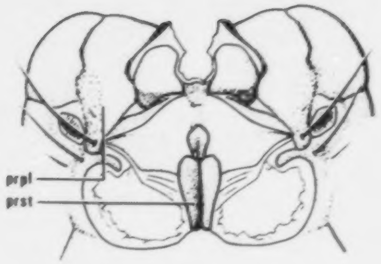
R4+5
M1
A1+CuA2
CuA1

3 Dryomyza anilis ♀



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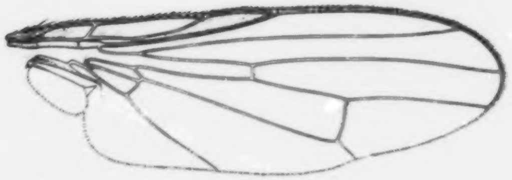
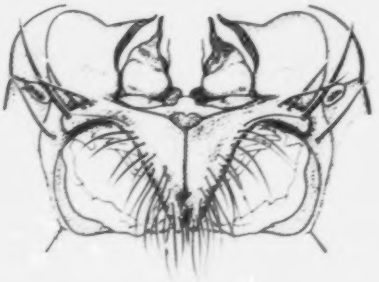
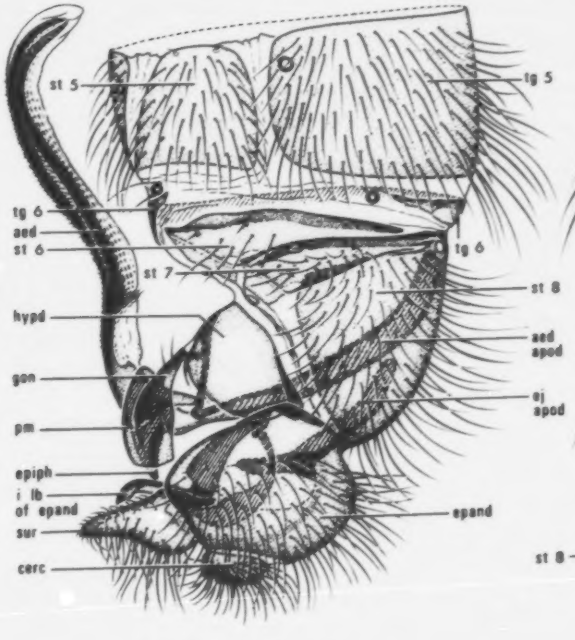


4 Heterocheila hannai ♀



6 Helcomyza mirabilis ♂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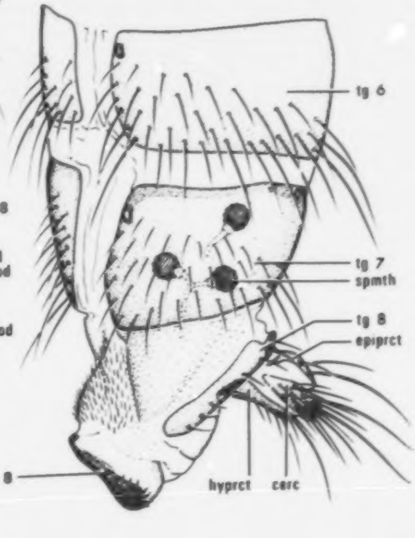
7 Dryomyza flaveola ♂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8 Dryomyza flaveola ♀

Figs. 83.3–8. Wings, thoraces, and abdomens: wings of (3) *Dryomyza anilis* Fallén and (4) *Heterocheila hannai* (Cole); prosternum and surrounding sclerites of (5) *Dryomyza anilis* and (6) *Helcomyza mirabilis* Melander; terminalia of (7) male and (8) female of *Dryomyza flaveola* (Fabricius), left lateral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gon, gonopod; hyprct, hypoproct; hypd, hypandrium; i lb of epand, inner lobe of epandrium; pm, paramere; prpl, propleuron; prst, prosternum; spmth, spermatheca; st, sternite; sur, surstylus; tg, tergite.

Key to genera

1. Prosternum strap-shaped or oval, well-separated by membrane from propleuron (Fig. 5). Crossvein bm-cu distinctly apical to CuA_2 (Fig. 3). Gena bare for at least half of distance from lower edge of eye to oral margin (Fig. 1). Antennae only narrowly separated basally. Wing without costal spines .... DRYOMYZINAE....2

Prosternum triangular, extending laterally to join propleuron (Fig. 6). Crossvein bm-cu almost in line with CuA_2 (Fig. 4). Gena haired almost to eye (Fig. 2). Antennae separated by at least diameter of scape. Wing sometimes with costal spines .... HELCOMYZINAE....3

2. Most of anepisternum with hairs. First flagellomere nearly circular. Body dark gray .... ***Oedoparena*** Curran

2 spp.; Alaska to California, coastal; Mathis and Steyskal 1980

Anepisternum bare. First flagellomere longer than wide. Body yellow to brown .... ***Dryomyza*** Fallén

7 spp.; widespread; Steyskal 1957

3. Mid tibia with a few nonapical posterodorsal and posterior setae. Wing with crossveins clouded; C with several short spines. Prosternum setulose .... ***Helcomyza*** Curtis

1 sp., *mirabilis* Melander; coasts of Oregon and Washington; Steyskal 1958

Mid tibia with dorsal, preapical, and apical setae only. Wing with crossveins unmarked; C with only fine setulae (Fig. 5). Prosternum bare .... ***Heterocheila*** Rondani

1 sp., *hannai* (Cole); Alaska; Steyskal 1958, as *Oedoparea buccata* (Fallén)

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SCIOMYZIDAE

84

LLOYD V. KNUTSON

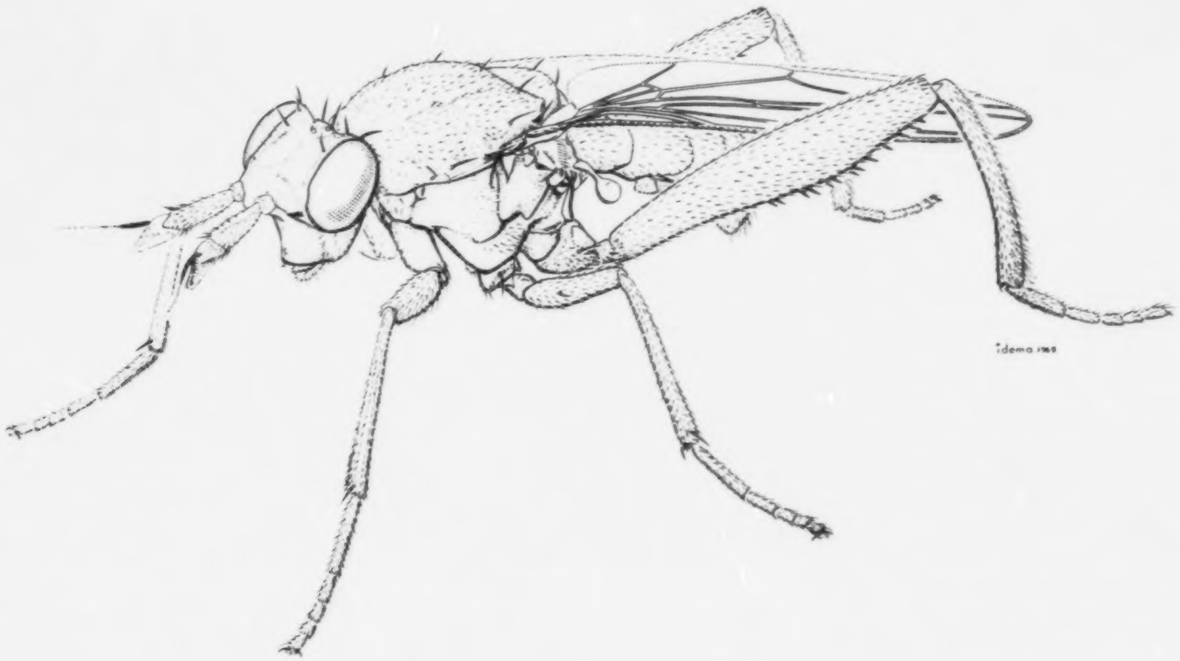


Fig. 84.1. Male of *Sepedon fuscipennis fuscipennis* Loew.

Small to moderately large, slender to robust flies (Fig. 1), ranging from 1.8 to 11.5 mm in length; color varying from shiny black to dull gray, brown, reddish, or yellowish; wing often patterned. Wing and abdomen of normal proportions; legs often somewhat elongate. Antenna porrect. Body usually not hairy, but bristles well-developed.

Adult. Head: as wide as or wider than thorax, with face usually concave in profile (Figs. 8–11, 13). Frontal vitta well-developed and shiny in most Tetanocerini, absent or reduced in most Sciomyzini; occasionally one, usually two orbital bristles present; ocellar bristles absent only in *Hedria* Steyskal, *Sepedon* Latreille, and *Sepedomerus* Steyskal; inner and outer vertical bristles well-developed; postocellar bristles strong, parallel or slightly divergent; vibrissae absent; subvibrissal setae mostly weak. Antenna porrect, short to elongate; arista short pubescent to plumose. Palpus narrow, elongate; proboscis moderately short.

Thorax: precoxal bridge absent. Postpronotal bristle usually present, but absent in *Sepedon* (Fig. 1) and some *Renocera* Hendel; presutural intra-alar bristle usually present; one supra-alar and one or two postalar bristles present; usually two but sometimes zero, one, or three postsutural dorsocentral bristles present; one prescutellar acrostichal bristle present or absent; usually two pairs of scutellar bristles present, although basal pair absent in *Sepedon*, some *Anticheta* Haliday, and *Hedria*; notopleuron with two bristles; proepisternal bristle well-developed in Sciomyzini, except in *Atrichomelina* Cresson, but absent in Tetanocerini; anepisternum, anepimeron, and katepisternum bare, or with hairs or bristles; subalar sclerite (vallar ridge) bare or with bristles, never densely pubescent.

Wing (Figs. 14–17) usually longer than abdomen, and immaculate or infumated along veins, spotted or heavily patterned. C not broken, without spines, extending to end of M_{1+2}; Sc complete, free from R_1 distally, and ending in C; crossvein dm-cu often sinuate; A_1 (A_1 + CuA_2) usually reaching wing margin, but abbreviated in *Colobaea* Zetterstedt (Fig. 14). Halter small to moderately long; calypteres small.

Hind coxa often with hairs posteromedially. Femora well-developed, usually strongly bristled. One or more tibiae with preapical dorsal bristle.

Abdomen: moderately long, cylindrical. Abdominal spiracles 1–5 situated in membrane; spiracles 6 and 7 usually in tergites.

Male with first five segments normal; tergites 1 and 2 fused. Traces of segments 6 and 7 present, free laterally from syntergosternite 8, and bearing spiracles 6 and 7 (Fig. 18), or entirely fused with syntergosternite enclosing spiracles 6 and 7, and ranging from asymmetric (e.g. *Pherbellia* Robineau-Desvoidy) to symmetric (e.g. *Sepedon*). A small sclerite possibly representing a remnant of tergite 8 sometimes present (Figs. 18, 19). Epandrium, hypandrium, and surstyli almost always symmetric. Epandrium hood-like. Surstylus usually divided into anterior and posterior lobes; anterior and posterior lobes well-developed in most Sciomyzini; only posterior lobe developed in most Tetanocerini (Figs. 19, 20), or posterior lobe and vestiges of anterior lobe present in some Tetanocerini; anterior lobe articulated at anteroventral angle of epandrium; posterior lobe articulated at posterior margin of epandrium. Cerci well-developed, setose. Sternite 10 usually developed as a flat sclerite or as a pair of sclerites. Hypandrium U-shaped, well-sclerotized, with a variably developed hypandrial bridge and apodeme; gonopod usually well-developed; aedeagus well-developed, usually membranous and flexible but occasionally well-sclerotized and complex (Fig. 19), usually asymmetric; aedeagal apodeme free, well-developed (Fig. 21); paramere strongly developed but usually small; sperm pump and ejaculatory apodeme present but sometimes weak.

Female abdomen composed of five normal segments and three reduced tergites and sternites; intersegmental membranes only moderately developed. Cerci small to moderately large; epiproct small; hypoproct distinct. Two sclerotized spermathecae present (Fig. 18), spherical or subspherical, on separate ducts; two accessory glands present.

All 72 species of Sciomyzini and Tetanocerini comprising 26 genera that have been examined cytologically have $2n = 12$ chromosomes, except for two species of *Pteromicra* Lioy, which have $2n = 10$, and *Sepedon spinipes americana* Steyskal, which has $2n = 11$ in male and $2n = 12$ in female (Boyes *et al.* 1972).

Egg. Elongate ovoid and white, yellowish, or grayish, usually unicolorous, rarely spotted. Chorion sculpturing finely reticulate or striate, occasionally with a few strong lateral grooves; lateral wings or terminal filaments absent. Micropyle terminal or subterminal and shielded by one to several tubercles or by an arched transverse lip; end opposite micropyle often a large conical punctate tubercle.

Larva. Third-instar elongate, cylindrical (Figs. 21, 22); anterior end strongly tapered and retractile; posterior end truncate, surrounded by two to five pairs of short to elongate fleshy lobes. Cuticle unpigmented and with spinules at least ventrally in Sciomyzini, or with a dense coat of transparent spinules in *Anticheta*, or entirely naked in terrestrial Tetanocerini, or pigmented and with rings of wart-like tubercles dorsally and laterally and with creeping welts ventrally in aquatic Tetanocerini (Figs. 18, 21–22).

No cuticular food canals (oral grooves) on ventral surface of first segment; mandibles without accessory teeth or with two to seven accessory teeth ventrally, slightly fused posterodorsally and connected ventrally by a curved anteriorly serrate ventral arch; no dental sclerites at ventral margins of mandibles. Labial sclerite (Fig. 31) usually present below posteroventral projections of mandibles, but absent in *Dictya* Meigen. Hypopharyngeal sclerite H- or V-shaped; posterior rami occasionally connected by transverse bar, and usually separate from tentoropharyngeal sclerite, never overlying anteroventral processes of tentoropharyngeal sclerite. Plate-like epipharyngeal sclerite fused posterolaterally with narrow parastomal bars. Anterodorsal bridge present between paired tentoropharyngeal sclerites; no tentoropharyngeal ridges in ventral floor. Dorsal and ventral cornua separated by a sinus extending one-third to three-quarters distance to anterior margin of sclerite; ventral cornu with window but without dorsobasal lobe; dorsal cornu with or without window.

Anterior spiracles stalked; apical portion rounded, lanceolate, or bifid in *Colobaea*; 4–32 spiracular papillae present. Paired posterior spiracles separate near center of posterior spiracular disc; each spiracle with three short oval radially arranged slits; spiracular hairs present or absent.

Puparium. Distinctively shaped. Those formed in water with posterior and occasionally anterior ends elevated above dorsal surface. Those formed in shoreline debris or ground litter cylindrical with anterior and posterior spiracles near middle of longitudinal axis. Those formed in snail shells often with anterior end flattened or with calcareous septum (produced by larva) between anterior end of puparium and opening of shell.

Biology and behavior. The biology and other aspects of Sciomyzidae have recently been reviewed on a world basis by Berg and Knutson (1978), and Fisher and Orth (1983) discuss the biology and taxonomy of 49 species found in California. Larvae of the approximately 200 species in 34 genera that have been reared from all regions of the world feed only on freshwater or terrestrial snails (including a few operculate species) or their eggs, or on slugs or fingernail clams (Sphaeriidae). More than 50 species of Sciomyzidae representing 12 genera have been associated in nature with 15 families comprising about 60 species of Mollusca. Larval feeding habits include predation, parasitoidism, and saprophagy; the behavioral modes are somewhat correlated with the taxonomic categories but the two do not coincide precisely. A few species of Sciomyzini, e.g. *Sciomyza aristalis* (Coquillett) (Foote 1959*a*), are highly specialized parasitoids that are intimately associated throughout their life cycle with snails, such as species of *Succinea* Draparnaud, in terrestrial situations. Females of these species search for the host and lay one or two eggs on the shell; usually only one larva feeds in each snail, so subtly that the host is not killed until the larva is almost completely developed. The puparium, often adapting its shape to fit, is formed in the shell of the snail. In contrast, most Tetanocerini, e.g. *Elgiva solicita* (Harris) (Knutson and Berg 1964), are overt predators of aquatic snails such as Lymnaeidae, Physidae, and Planorbidae. Eggs are laid on emergent vegetation, and the larva actively searches for its prey. During its development, the larva kills as many as 30 snails; each snail is killed quickly and only partially eaten. The puparium is formed in the water and is morphologically adapted for flotation. Between these two extremes, many species of both tribes exhibit intermediate and mixed behavior. Most feed on aquatic snails that are at the shoreline or otherwise exposed. A few species of *Tetanocera* Duméril and *Euthycera* Latreille are the only typical Tetanocerini known that have an atypical food preference, namely slugs. Two morphologically atypical genera, usually placed in the Tetanocerini, have the most irregular habits: *Anticheta*, e.g. *A. testacea* Melander (Fisher and Orth 1964), is restricted to feeding on eggs of Lymnaeidae, Physidae, or Succineidae during early stages, and all known *Renocera* feed only on fingernail clams (Foote 1976). Five distinct patterns of seasonality, overwintering, and voltinism in Sciomyzidae living in cool, temperate latitudes were described by Berg *et al.* (1982). Premating behavior by species of *Sepedon* was described by Berg and Valley (1985*a*, 1985*b*).

Classification and distribution. The world fauna is composed of about 60 genera and 550 species, with rather high levels of endemism in all regions. The Nearctic and Palaearctic faunas are taxonomically the most diverse and contain the most species, although the Neotropical fauna also is moderately well-developed (23 genera and at least 74 species). Catalogs were recently published for the Nearctic (Knutson *et al.* 1986) and the Palaearctic (Rozkošný and Elberg 1984). The Afrotropical region is dominated by *Sepedon* and related genera. Several aberrant genera occur in the Australian region. The Oriental and eastern Palaearctic faunas are the least well known. The North American fauna comprises 21 genera and at least 174 species and is restricted to one subfamily, the Sciomyzinae; the other subfamilies are Palaearctic, Afrotropical, and Australian. The Sciomyzinae consists of two tribes, the Sciomyzini and the Tetanocerini of Steyskal (1965) (=Sciomyzinae and Tetanocerinae of earlier literature); the Tetanocerini contains about two-thirds of the North American species. *Sciomyza florissantensis* Cockerell, the only known fossil species from North America, was described from the Miocene shales of Colorado (Cockerell 1909).

Keys to genera

Adult

1. Proepisternal bristle well-developed; if this bristle hair-like, then first tarsomere of foreleg white and other tarsomeres black .... SCIOMYZINI....2

Proepisternal bristle absent .... TETANOCERINI....7

2. Proepisternal bristle hair-like. First tarsomere of foreleg white and other tarsomeres black; fore coxa without bristles. All thoracic pleurites with hairs, but without bristles .... ***Atrichomelina*** Cresson

1 sp., *pubera* (Loew); southernmost Canada, throughout U.S.A., south to Tamaulipas, Distrito Federal, and Chiapas, Mexico

Proepisternal bristle well-developed. First tarsomere of foreleg at most yellowish and other tarsomeres brownish; fore coxa with one or more bristles. At least one thoracic pleurite bare or with one or more bristles 3

3. Fore tibia with one preapical dorsal bristle 4

Fore tibia with two preapical dorsal bristles 6

4. A_1 (=A_1 + CuA_2) not reaching margin of wing (Fig. 14). Frons dull black. Arista with a few dorsobasal hairs much longer than others (Fig. 2) .... ***Colobaea*** Zetterstedt

1 sp., *americana* Steyskal; Manitoba, Quebec, New York

A_1 reaching margin of wing, though sometimes faint apically (Figs. 15–17). Frons dull yellow or entirely shiny, never dull black. Arista never with elongate dorsobasal hairs (Fig. 3) 5

5. Frons entirely shiny. Fore femur usually with a short series of closely spaced spinules (pecten) anteromedially (Fig. 12). Thorax shiny black or brown .... ***Pteromicra*** Lioy

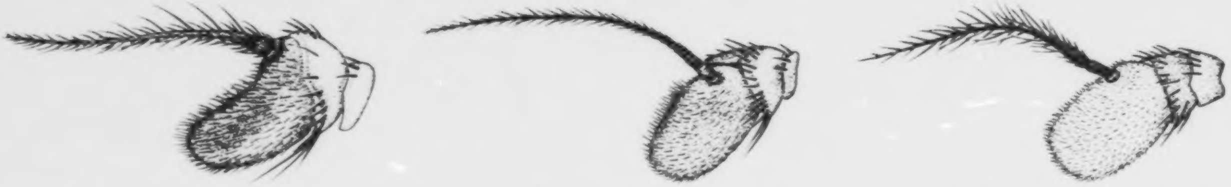
14 spp.; Alaska, Canada, northern and western U.S.A.; Foote 1959*b*; Fisher and Orth 1966; Knutson 1971; Knutson and Zuska 1968; Rozkošný and Knutson 1970; Steyskal 1954*b*, 1954*c*, 1957

Frons not shiny. Fore femur without a series of closely spaced spinules (pecten). Thorax pruinose yellow, brown, or gray .... ***Pherbellia*** Robineau-Desvoidy

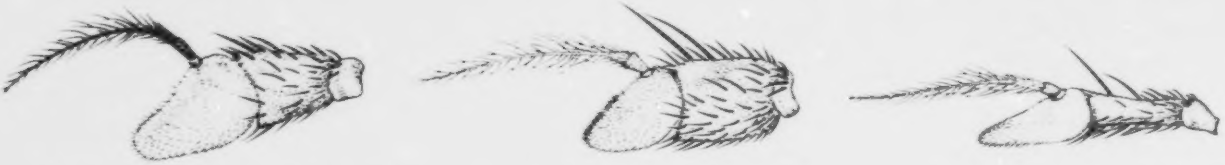
40 spp.; widespread; Steyskal 1949, 1961, 1963, 1966; Orth *et al.* 1980; Orth and Steyskal 1981; Orth 1982, 1983, 1984

6. Arista black. Two orbital bristles present; presutural intra-alar (posthumeral) bristle present; two postsutural dorsocentral bristles present. Face not tuberculate (Fig. 8) .... ***Sciomyza*** Fallén

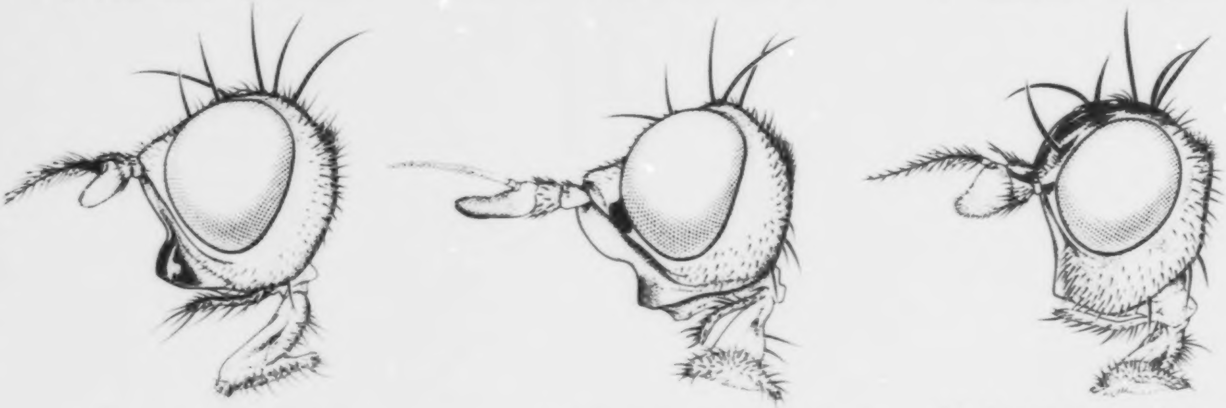
4 spp.; Alaska, Canada, and western, central, and northeastern U.S.A.; Steyskal 1954*b*



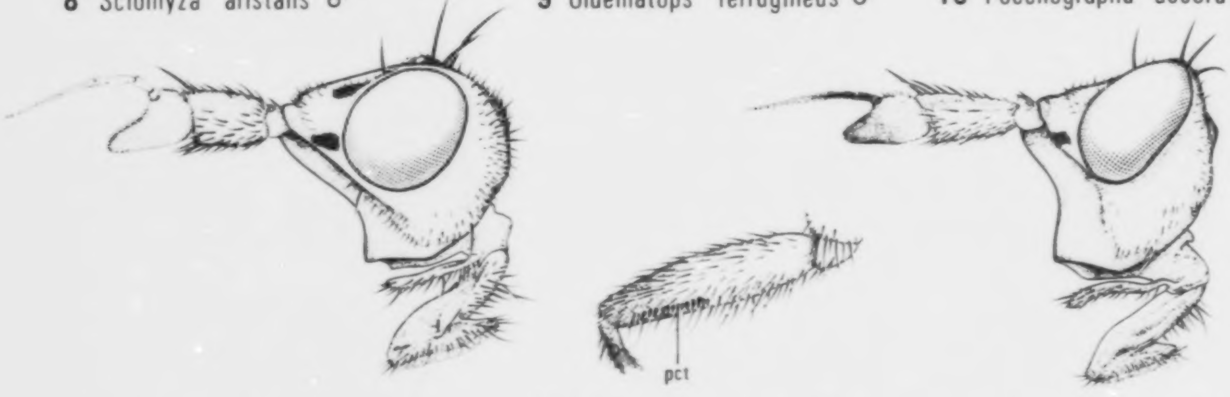
2 Colobaea americana ♂ **3** Pherbellia maculata ♂ **4** Renocera brevis ♀



5 Tetanocera griseicollis ♀ **6** Euthycera arcuata ♀ **7** Dictyacium ambiguum ♀



8 Sciomyza aristalis ♂ **9** Oidematops ferrugineus ♂ **10** Poecilographa decora ♀



11 Hedria mixta ♀ **12** Pteromicra pleuralis ♂ **13** Sepedon fuscipennis fuscipennis ♀

Figs. 84.2–13. Antennae, heads, and leg: antennae of (2) *Colobaea americana* Steyskal, (3) *Pherbellia maculata* (Cresson), (4) *Renocera brevis* (Cresson), (5) *Tetanocera griseicollis* (Becker), (6) *Euthycera arcuata* (Loew), and (7) *Dictyacium ambiguum* (Loew); heads of (8) *Sciomyza aristalis* (Coquillett), (9) *Oidematops ferrugineus* Cresson, (10) *Poecilographa decora* (Loew), and (11) *Hedria mixta* Steyskal; (12) fore femur of *Pteromicra pleuralis* (Cresson); (13) head of *Sepedon fuscipennis fuscipennis* Loew.

Abbreviation: pct, pecten.

Arista white. One orbital bristle present; presutural intra-alar bristle absent; one postsutural dorsocentral bristle present. Face tuberculate (Fig. 9) . . . . ***Oidematops*** Cresson

1 sp., *ferrugineus* Cresson; east central North America

7. Ocellar bristles present and crossvein dm-cu straight to slightly curved. Presutural intra-alar bristle usually present 8

Ocellar bristles usually absent (hair-like in some specimens of some species of *Sepedon*), but if well-developed (*Elgiva*), crossvein dm-cu bent almost at right angles. Presutural intra-alar bristle usually absent 18

8. Frons strongly convex, glossy (Fig. 10). Three postsutural dorsocentral bristles present, one at suture. Body yellowish with dark spots. Wing patterned (Fig. 15) . . . . ***Poecilographa*** Melander

1 sp., *decora* (Loew); east central North America

Frons not strongly convex, occasionally shiny. One to four postsutural dorsocentral bristles present. Body shining black or dull brownish to gray, with or without spots. Wing patterned or not 9

9. Subalar sclerite without vallar bristles 10

Subalar sclerite with vallar bristles 16

10. Hind tibia with two preapical dorsal bristles. Only katepisternum with hairs. Arista black . . . . ***Anticheta*** Haliday

9 spp.; western, central, and northern U.S.A. and southern Canada; Steyskal 1960*b*, Fisher and Orth 1971

Hind tibia with one preapical dorsal bristle. One or more thoracic pleurites with hairs or bristles. Arista black or white 11

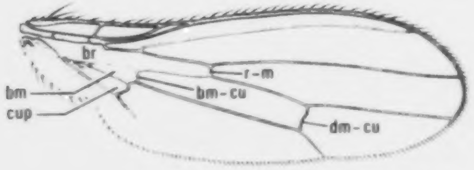
11. Pedicel less than one-third length of first flagellomere (Fig. 4); arista black. Wing not patterned . . . . ***Renocera*** Hendel

4 spp.; northern U.S.A., southern Canada; Melander 1920, Foote 1976

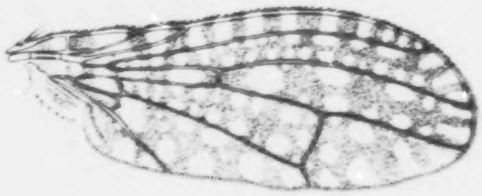
Pedicel at least one-half length of first flagellomere; arista black or white. Wing patterned or not 12

12. Anepisternum and anepimeron with bristles; one orbital bristle or three dorsocentral bristles present 13

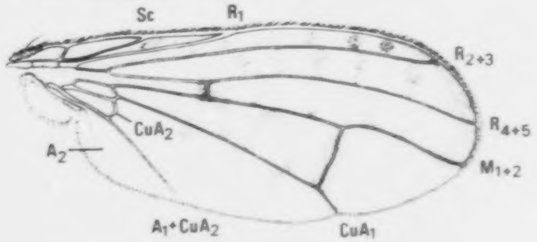
Anepisternum and anepimeron bare or with hairs; two orbital bristles and two dorsocentral bristles present 14



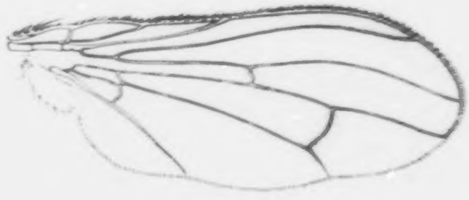
14 Colobaea americana ♂



15 Poecilographa decora ♀

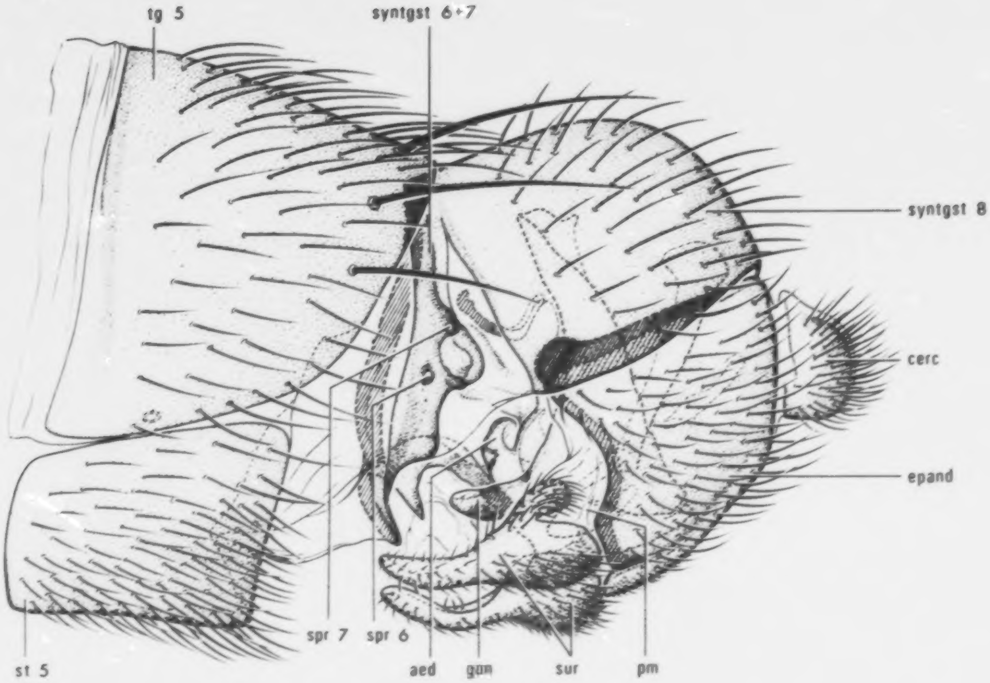


16 Tetanocera valida ♀

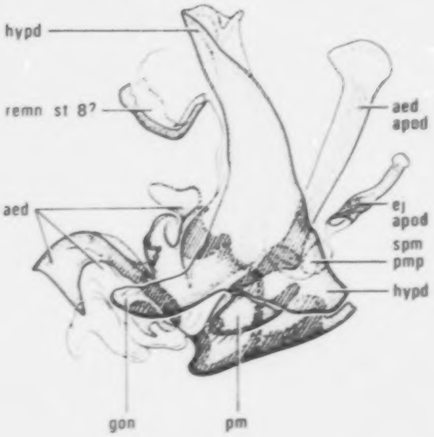


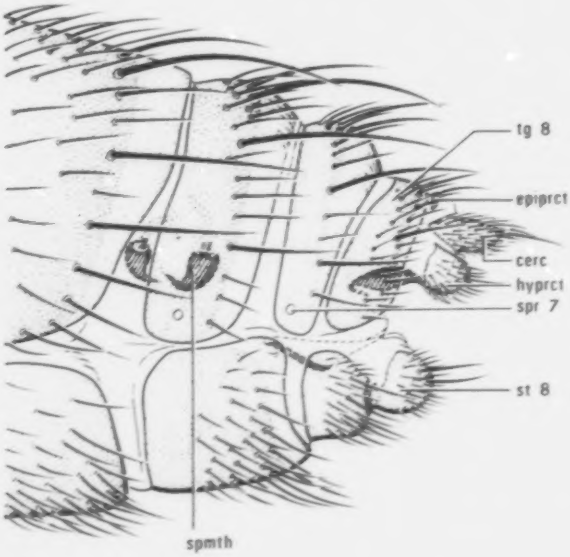
17 Tetanocera plebeja ♀

Figs. 84.14–17. Wings: (14) *Colobaea americana* Steyskal; (15) *Poecilographa decora* (Loew); (16) *Tetanocera valida* Loew; (17) *Tetanocera plebeja* Loew.


tg 5
syntgst 6+7
syntgst 8
cerc
epand
st 5
spr 7
spr 6
aed
gon
sur
pm

18 Tetanocera plebeja ♂


hypd
remn st 8?
aed
aed apod
ej apod
spm pmp
hypd
gon
pm

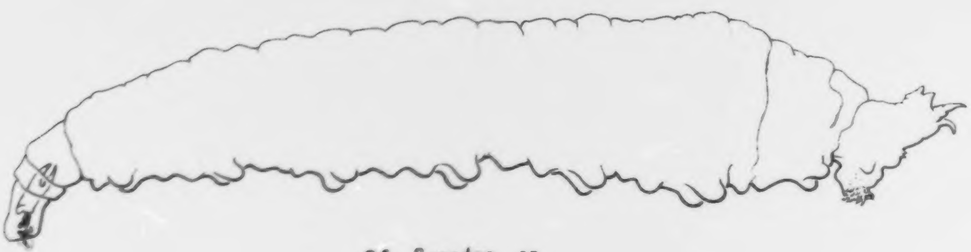

tg 8
epiprct
cerc
hyprct
spr 7
st 8
spmth

19 Tetanocera plebeja ♂

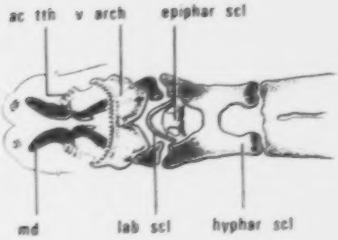
20 Tetanocera plebeja ♀

Figs. 84.18–20. Terminalia of *Tetanocera plebeja* Loew: (18) ventrolateral view of male; (19) lateral view of internal structures of male; (20) lateral view of female.

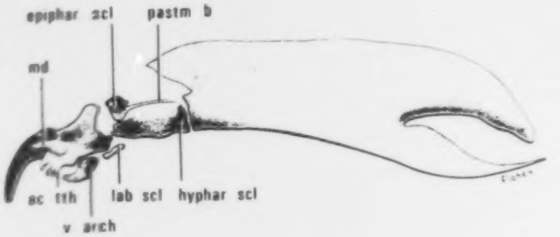
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; remn tg 8?, possible remnant of tergite 8; spm pmp, sperm pump; spmth, spermatheca; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.



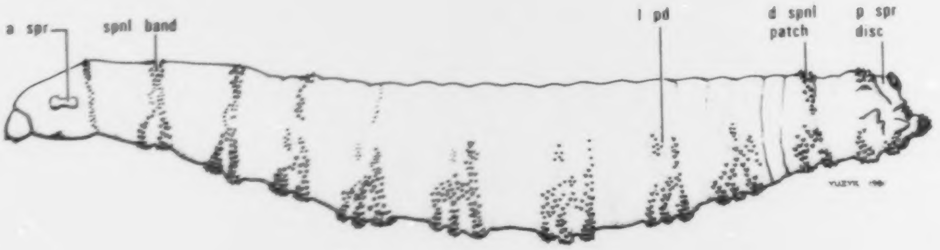
21 Sepedon sp.


ac tth
v arch
epiphar scl
md
lab scl
hyphar scl

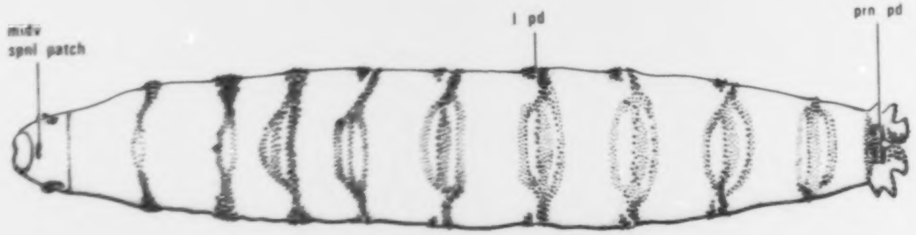
22 Sepedon sp.


epiphar scl
pastm b
md
ac tth
v arch
lab scl
hyphar scl

23 Sepedon sp.


a spr
spnl band
l pd
d spnl patch
p spr disc

24 Pherbellia dorsata


midv spnl patch
l pd
prn pd

25 Pherbellia dorsata

Figs. 84.21–25. Larvae and larval mouthparts: (21) lateral view of third instar larva of *Sepedon* sp.; (22) ventral view and (23) lateral view of cephalopharyngeal skeleton of *Sepedon* sp.; (24) lateral view and (25) ventral view of third instar larva of *Pherbellia dorsata* (Zetterstedt). Figs. 24 and 25 redrawn from Bratt *et al.* (1969).

Abbreviations: ac tth, accessory teeth; a spr, anterior spiracle; d spnl patch, dorsal spinule patch; epiphar scl, epipharyngeal sclerite; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; l pd, lateral pad; md, mandible; midv spnl patch, midventral spinule patch; pastm b, parastomal bar; prn pd, perianal pad; p spr disc, posterior spiracular disc; spnl band, spinule band; v arch, ventral arch.

13. Face white, without central black spot; two orbital bristles present. Three dorsocentral bristles present; all thoracic pleurites bristled .... ***Hoplodictya*** Cresson
5 spp.; southernmost Canada, U.S.A., southward to Guatemala; Fisher and Orth 1972*b*

Face white, with central black spot; one orbital bristle present. Two dorsocentral bristles present; katepisternum with hairs but without bristles .... ***Dictya*** Meigen
25 spp.; throughout North America, Bahama Islands, Bermuda, south to Costa Rica; Steyskal 1954*a*, Fisher and Orth 1969*b*, Valley and Berg 1977, Orth and Fisher 1983

14. Arista black. Wing usually not patterned, at most sparsely patterned with discrete dark spots (Figs. 16–17) .... ***Tetanocera*** Duméril
30 spp.; most abundant in northern U.S.A. and Canada; Steyskal 1959, Orth and Fisher 1982

Arista white. Wing densely patterned with dark network around hyaline spots 15

15. Face flat to slightly concave. Pedicel less than twice as long as wide, compressed (Fig. 6) .... ***Euthycera*** Latreille
1 sp., *arcuata* (Loew); U.S.A. and southern Canada east of Rocky Mountains

Face tuberculate. Pedicel twice as long as wide, cylindrical (Fig. 7) .... ***Dictyacium*** Steyskal
2 spp.; northern and central U.S.A. and southern Canada mainly east of Rocky Mountains; Steyskal 1956

16. Prescutellar acrostichal bristles absent. Mid tibia without distinct preapical dorsal bristle. Prosternum bare and arista black .... ***Pherbecta*** Steyskal
1 sp., *limenitis* Steyskal; northeastern U.S.A., southeastern Canada; Knutson 1972

Prescutellar acrostichal bristles present. Mid tibia with at least one distinct preapical dorsal bristle. Prosternum bare or haired and arista white, or prosternum haired and arista black . . . 17

17. Arista white. Frontal vitta broad, shiny. Anepisternum and anepimeron with hairs but without bristles .... ***Limnia*** Robineau-Desvoidy
17 spp.; widespread; Steyskal *et al.* 1978

Arista black. Frontal vitta narrow, waxy. Anepisternum and anepimeron with hairs and some bristles .... ***Trypetoptera*** Hendel
1 sp., *canadensis* (Macquart); northern U.S.A., southern Canada

18. Ocellar bristles present, well-developed. Two pairs of scutellar bristles present. Hind coxa with hairs posteromedially. Crossvein dm-cu strongly bent .... ***Elgiva*** Meigen
2 spp.; Alaska, Canada, northern U.S.A.; Steyskal 1954*b*

Ocellar bristles absent (hair-like in some specimens of some species of *Sepedon*). One or two pairs of scutellar bristles present. Hind coxa usually without hairs posteromedially. Crossvein dm-cu straight to curved 19

19. Two orbital bristles present, the anterior one smaller. Postpronotal bristle present. Head as in Fig. 11. Crossvein dm-cu S-shaped .... ***Hedria*** Steyskal
1 sp., *mixta* Steyskal; Canada, northern U.S.A.

One orbital bristle present. Postpronotal bristle absent. Head as in Fig. 13. Crossvein dm-cu straight to arched 20

20. Postocellar bristles absent. Mid femur with minute bristles, none of which is distinctly larger than the others .... ***Sepedomerus*** Steyskal
1 sp., *macropus* Walker; Texas, West Indies, Central and South America; Steyskal 1973

Postocellar bristles well-developed. Mid femur with one or more distinctly larger anterior setae near midlength of femur .... ***Sepedon*** Latreille
16 spp.; widespread; Steyskal 1951, 1956, 1960*a*; Fisher and Orth 1969*a*, 1972*a*, 1974; Orth 1986

Larva[1]
(third instar)

1. Indentation index (distance *a b* ÷ *c d* × 100, Fig. 26) much more than 50. Mandible without accessory teeth (Fig. 26); hypopharyngeal and tentoropharyngeal sclerites separate (Fig. 26); dorsal bridge present between tentoropharyngeal sclerites; dorsal and ventral cornua of tentoropharyngeal sclerite with windows (as in Fig. 27). Ventral spinule patches present; no well-developed body tubercles or elongate lobes around posterior spiracular disc (Fig. 37); no spiracular hairs on posterior spiracular plates .... SCIOMYZINI 2

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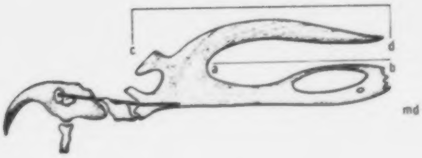
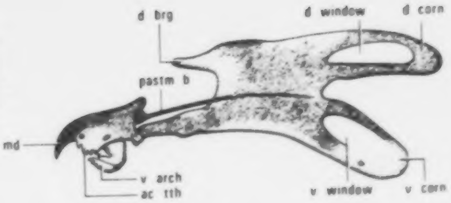
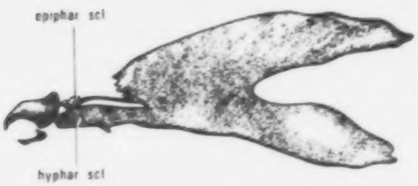
[1] The larvae of *Dictyacium*, *Poecilographa*, and *Trypetoptera* are unknown.



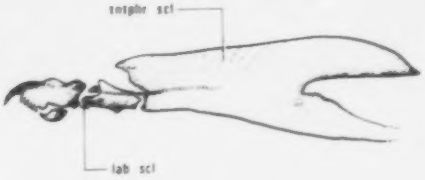
26 Atrichomelina pubera



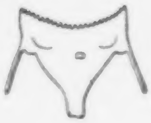
27 Anticheta testacea



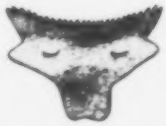
28 Renocera sp.



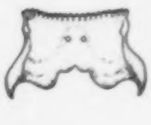
29 Elgiva solicita



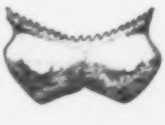
30 Hoplodictya spinicornis



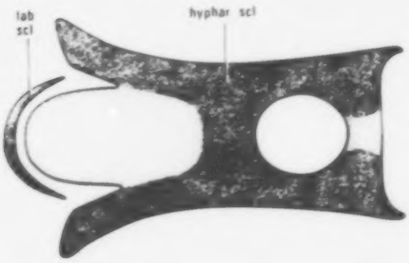
31 Dictya expansa



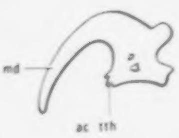
32 Sepedon tenuicornis



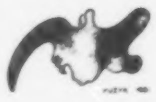
33 Elgiva solicita



34 Elgiva solicita



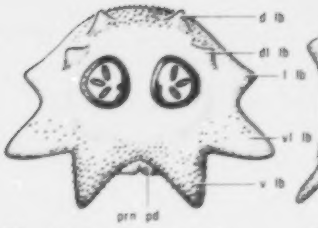
35 Euthycera arcuata



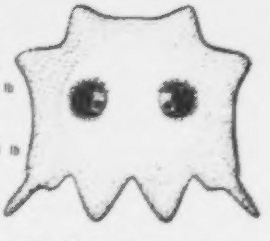
36 Sepedon tenuicornis

Figs. 84.26–36. Larval mouthparts: Cephalopharyngeal skeleton of (26) *Atrichomelina pubera* (Loew), (27) *Anticheta testacea* Melander, (28) *Renocera* sp., and (29) *Elgiva solicita* (Harris); ventral arch of (30) *Hoplodictya spinicornis* (Loew), (31) *Dictya expansa* Steyskal, (32) *Sepedon tenuicornis* Cresson, and (33) *Elgiva solicita*; (34) labial and hypopharyngeal sclerites of *Elgiva solicita*; mandible of (35) *Euthycera arcuata* (Loew) and (36) *Sepedon tenuicornis*. Fig. 26 redrawn from Foote *et al.* (1960). Fig. 27 redrawn from Fisher and Orth (1964). Fig. 28 from B. A. Foote, unpublished. Figs. 29, 33, and 34 redrawn from Knutson and Berg (1964). Fig. 30 redrawn from Neff and Berg (1962). Fig. 31 redrawn from Valley and Berg (1977). Figs. 32 and 36 redrawn from Neff and Berg (1966). Fig. 35 redrawn from Knutson (1963).

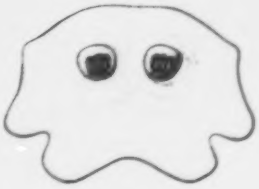
Abbreviations: ab ÷ cd × 100, indentation index; ac tth, accessory teeth; d brg, dorsal bridge; d corn, dorsal cornu; d window, dorsal window; epiphar scl, epipharyngeal sclerite; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; pastm b, parastomal bar; tntphr scl, tentoropharyngeal sclerite; v arch, ventral arch; v corn, ventral cornu; v window, ventral window.



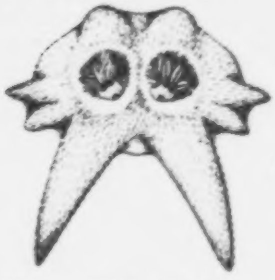
37 Atrichomelina pubera



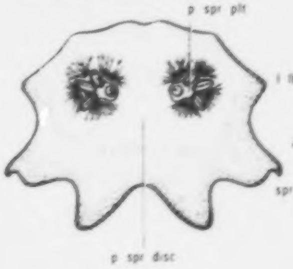
38 Tetanocera montana



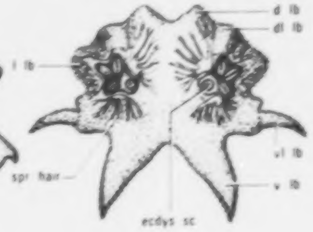
39 Hoplodictya spinicornis



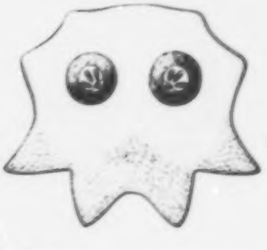
40 Hoplodictya setosa



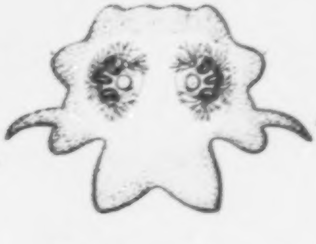
41 Sepedon relictus



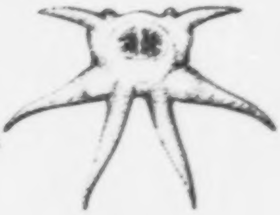
42 Sepedon tenuicornis



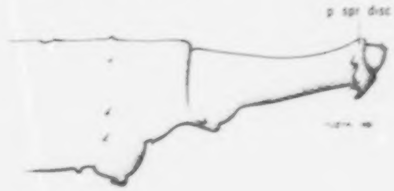
43 Tetanocera phyllophora



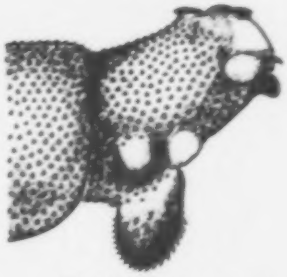
44 Dictya matthewsi



45 Hedria mixta



46 Elgiva solicita



47 Tetanocera montana

Figs. 84.37–47. Larval structures: posterior spiracular disc of (37) *Atrichomelina pubera* (Loew), (38) *Tetanocera montana* Day, (39) *Hoplodictya spinicornis* (Loew), (40) *Hoplodictya setosa* (Coquillett), (41) *Sepedon relictus* Wulp, (42) *Sepedon tenuicornis* Cresson, (43) *Tetanocera phyllophora* Melander, (44) *Dictya matthewsi* Steyskal, and (45) *Hedria mixta* Steyskal; abdominal segments 7 and 8 of (46) *Elgiva solicita* (Harris) and (47) *Tetanocera montana*. Fig. 37 redrawn from Foote *et al.* (1960). Figs. 38 and 43 redrawn from Knutson (1963). Figs. 39 and 40 redrawn from Neff and Berg (1962). Figs. 41 and 42 redrawn from Neff and Berg (1966). Fig. 44 redrawn from Valley and Berg (1977). Fig. 45 redrawn from Foote (1971). Fig. 46 redrawn from Knutson and Berg (1964). Fig. 47 redrawn from Foote (1961).

Abbreviations: d lb, dorsal lobe; dl lb, dorsolateral lobe; ecdys sc, ecdysial scar; l lb, lateral lobe; prn pd, perianal pad; p spr disc, posterior spiracular disc; p spr plt, posterior spiracular plate; spr hair, spiracular hair (bristle); v lb, ventral lobe; vl lb, ventrolateral lobe.

Indentation index usually 34–46 (Fig. 27). Mandible usually with accessory teeth (Figs. 23, 27, 29), but if these teeth absent, e.g. *Renocera* (Fig. 28), hypopharyngeal and tentoropharyngeal sclerites fused and indentation index about 50; dorsal bridge usually absent (Fig. 28), but present in *Anticheta* (Fig. 27). Ventral spinule patches usually absent, but if patches present, e.g. *Anticheta*, cuticle with dense coat of transparent spinules and indentation index about 50; well-developed body tubercles often present; elongate lobes around posterior spiracular disc often present, and spiracular hairs usually present (Figs. 44, 45) .... TETANOCERINI 5

2. Anterior spiracles bifid. Feeding on *Gyraulus* Charpentier .... ***Colobaea***

1 sp., *americana* Steyskal

Anterior spiracles circular, not divided. Feeding on aquatic or terrestrial snails 3

3. Lobes of posterior spiracular disc reduced, with only ventral lobes distinct; disc flattened in lateral view; posterior spiracular tubes barely projecting 4

At least ventrolateral lobes, in addition to ventral lobes, of posterior spiracular disc distinct (Fig. 37). Feeding on aquatic and terrestrial snails .... ***Atrichomelina***

1 sp., *pubera* (Loew); Foote *et al.* 1960

.... ***Pherbellia***

19 of 40 spp. known; Bratt *et al.* 1969

.... ***Pteromicra***

9 of 14 spp. known; Rozkošný and Knutson 1970

4. Anterior spiracles with 24–32 papillae. Feeding on Succineidae and Lymnaeidae .... ***Sciomyza***

3 of 4 spp. known; Foote 1959*a*

Anterior spiracles with 12 papillae. Feeding on *Stenotrema hirsutum* (Say) .... ***Oidematops***

1 sp., *ferrugineus* Cresson; Foote 1977

5. Indentation index about 50. Ventral spinule patches present or accessory teeth absent; hypopharyngeal and tentoropharyngeal sclerites fused (Figs. 27, 28) 6

Indentation index 34–46. Ventral spinule patches absent and accessory teeth present; hypopharyngeal and tentoropharyngeal sclerites separate (Fig. 29) 7

6. Accessory teeth and dorsal bridge present (Fig. 27). Cuticle thick, with ventral spinule patches and dense coat of large transparent spinules. Feeding on eggs of Succineidae, Lymnaeidae, and Physidae .... ***Anticheta***

4 of 9 spp. known; Fisher and Orth 1964, Knutson and Abercrombie 1977, Robinson and Foote 1978

Accessory teeth and dorsal bridge absent (Fig. 28). Cuticle normal, without ventral spinule patches and dense coat of large transparent spinules. Feeding on Sphaeriidae .... ***Renocera***

3 of 4 spp. known; Foote 1976

7. Ventral arch triangular to quadrate, with posteromedial projection (Figs. 30, 31); posteroventral margins of basal parts of mandibles curved medially, meeting posteromedial projection of ventral arch. Indentation index 34–37 8

Ventral arch bilobate, emarginate posteriorly (Figs. 32, 33); posteroventral margins of basal parts of mandibles not curved medially, remote from ventral arch. Indentation index 34–36 10

8. Labial sclerite absent; two or three accessory teeth present. Spiracular hairs present; 4–17 anterior spiracular papillae present; integument dark golden brown to brownish black; eight lobes on posterior spiracular disc (Fig. 44). Feeding on freshwater snails .... ***Dictya***

20 of 25 spp. known; Valley and Berg 1977

Labial sclerite present, occasionally reduced. Other characters variable 9

9. Three or four accessory teeth present on or near horizontal axis; labial sclerite reduced. Ten anterior spiracular papillae present; spiracular hairs absent; four lobes on posterior spiracular disc .... ***Pherbecta***

1 sp., *limenitis* Steyskal; Knutson 1972

One to three accessory teeth on or near vertical axis; labial sclerite well-developed; ventral arch with sclerotized posterolateral processes (Fig. 30). Five to nine anterior spiracular papillae present; spiracular hairs present or absent; eight or ten lobes on posterior spiracular disc (Fig. 40). Feeding on Succineidae and *Littorina litorea* (Linnaeus) .... ***Hoplodictya***

2 of 5 spp. known; Neff and Berg 1962

10. Basal part of mandible short, about one-half length of hypopharyngeal sclerite (Fig. 35); two accessory teeth present. Indentation index 46. Cuticle not pigmented; spiracular hairs absent. Feeding on terrestrial snails .... ***Euthycera***
1 sp., *arcuata* (Loew)

Basal part of mandible normal, about equal in length to hypopharyngeal sclerite (Fig. 36); more than two accessory teeth present. Cuticle pigmented or not; spiracular hairs present or absent. Feeding on aquatic or terrestrial snails 11

11. Three or four accessory teeth present; posterior rami of hypopharyngeal sclerite connected; ventral arch with sclerotized posterolateral projections (Fig. 32). Indentation index 34–36. Ten lobes on posterior spiracular disc (Fig. 42); spiracular hairs present; 4–12 anterior spiracular papillae present. Feeding on freshwater snails .... ***Sepedon***
12 of 19 spp. known; Neff and Berg 1966 ***Sepedomerus***

Ventral arch without posterolateral projections. Eight lobes on posterior spiracular disc 12

12. Five to seven accessory teeth present; posterior rami of hypopharyngeal sclerite connected. Indentation index 38. Postanal portion of abdominal segment 8 much longer than wide (Fig. 46); spiracular hairs present; 6–13 anterior spiracular papillae present. Feeding on freshwater snails .... ***Elgiva***
2 spp.; Knutson and Berg 1964

Two to seven accessory teeth present; posterior rami of hypopharyngeal sclerite usually not connected. Postanal portion of abdominal segment 8 not much longer than wide (Fig. 47); spiracular hairs usually present; 9–14 anterior spiracular papillae present. Indentation index 38–46. Feeding on freshwater or terrestrial snails or on slugs 13

13. Four accessory teeth present; posterior rami of hypopharyngeal sclerite not connected. Indentation index 38–40. Lateral, ventrolateral, and ventral lobes of posterior spiracular disc elongate, subequal (Fig. 45); lateral tubercle above anal proleg elongate, acute; spiracular hairs present; 10–14 anterior spiracular papillae present. Feeding on freshwater snails .... ***Hedria***
1 sp., *mixta* Steyskal; Foote 1971

Two to seven accessory teeth present. Indentation index 40–46. Lateral lobes of posterior spiracular disc always much shorter than ventrolateral and ventral lobes (Figs. 43, 44); lateral tubercle above anal proleg short, rounded (Fig. 47) 14

14. Cuticle not pigmented; spiracular hairs absent; 11–14 anterior spiracular papillae present; feeding on Succineidae, terrestrial snails, slugs. *Or* cuticle pigmented and spiracular hairs present; feeding on aquatic snails .... ***Tetanocera***
18 of 30 spp. known; Foote 1961, Knutson 1963, Trelka and Foote 1970

Cuticle not pigmented; spiracular hairs present; nine anterior spiracular papillae present. Four to seven accessory teeth present; posterior rami of hypopharyngeal sclerite not connected. Feeding on Succineidae .... ***Limnia***
1 of 17 spp. known

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ROPALOMERIDAE

85

GEORGE C. STEYSKAL

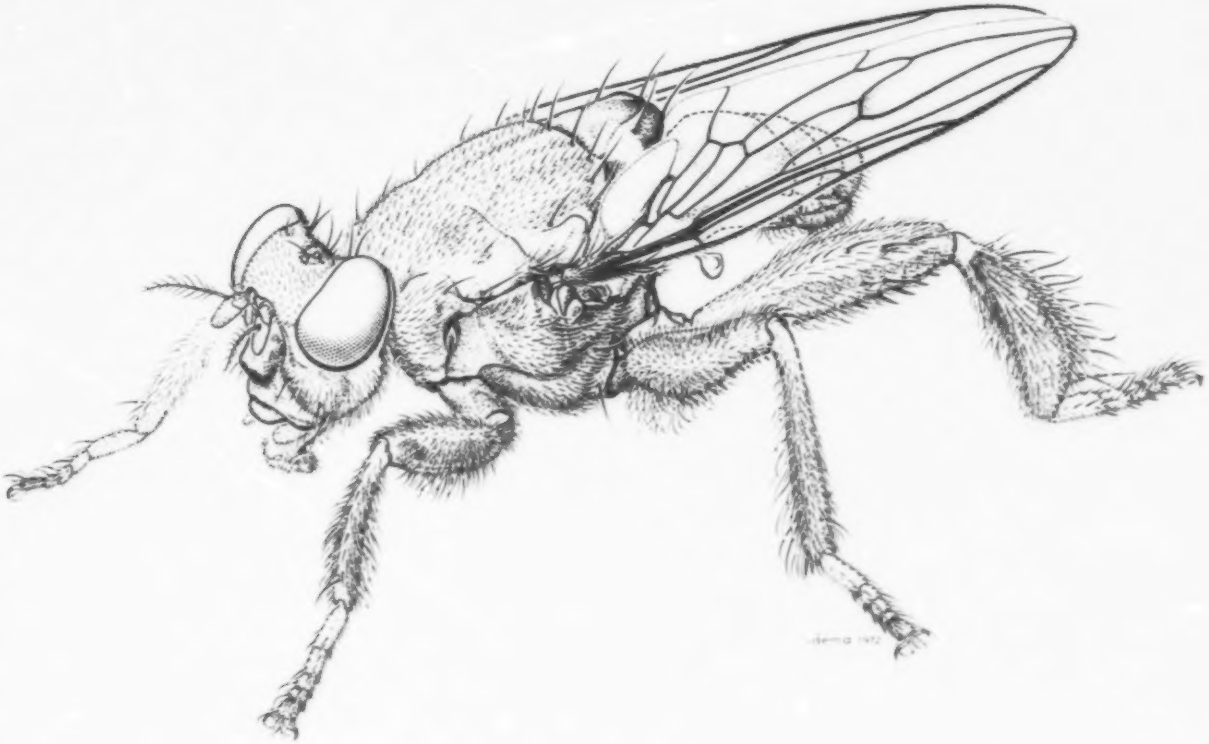


Fig. 85.1. Adult male of *Ropolomera femorata* (Fabricius) (Neotropical).

Robust flies (Fig. 1), of medium to rather large size, 6–12 mm in body length, generally brownish to dark brown in color. Wing from nearly plain hyaline or brownish to strongly spotted or blotched with dark brown. Femora, especially hind femur, conspicuously enlarged; hind tibia often laterally flattened and broadened.

Adult. Head: higher than long (Figs. 2–4), with eyes extending above vertex, and with cheek rather high. Face with median ridge or protuberance. Antenna with short scape and pedicel; first flagellomere ovoid or rather elongate; arista subbasal, slender, bare (Fig. 3) to plumose (Fig. 4) or covered with flattened hairs (*Mexicoa* Steyskal) (Fig. 2). Proboscis moderate; palpus more or less flattened and broadened. Chaetotaxy: one inner and one outer vertical bristle present, usually with one or two short orbital bristles; frontal bristles usually scarcely distinguishable from adjacent setulae; usually one small ocellar bristle and one divergent postocellar bristle present; vibrissae absent; subvibrissal bristles sometimes rather large.

Thorax: robust (Fig. 1). Scutellum sometimes a little elongate, with longitudinal channel; subscutellum present but weak; anepimeron with a strongly developed greater ampulla. Chaetotaxy: disc of proepisternum hairy; proepisternal and proepimeral bristles absent; one katepisternal and one or more anepisternal bristles present; one or more anepimeral bristles present or with a group of strong setulae; zero or one postpronotal and two notopleural bristles present; one presutural supra-alar bristle usually present; postsuturally with one supra-alar, one postalar, one intra-alar, and one dorsocentral bristle; sometimes one acrostichal and one to four scutellar bristles present; one or several distinct setae present on posterior margin of posterior spiracle.

Legs robust (Fig. 1); femora, especially hind femur, distinctly swollen; mid femur gently concave dorsally; all femora sometimes having strong setae ventrally. Tibiae somewhat thicker than tarsi; hind tibia often flattened laterally and curved, often with dorsal ridge and one or more rows of longish erect setae, and in the Neotropical genus *Lenkokroeberia* Prado a dense rather short dorsal fringe present.

Wing (Fig. 1) often somewhat pointed, hyaline to brown, frequently with dark bars or blotches or with pale areas. C without costal breaks; Sc complete, joining C well basal of R_1; M curved anteriorly to crossvein r-m, then angling posteriorly to crossvein dm-cu, then angling anteriorly to end at or a little anterior of wing tip; crossvein dm-cu oblique, more or less in line with last section of M; cell cu*p* shorter than cell bm, and closed by a virtually straight CuA_2 usually at right angles to length of cell cu*p*, but sometimes a little oblique, making posterodistal angle of cell cu*p* acute. All longitudinal veins complete to wing margin. Lower calypter moderately strongly developed.

Abdomen: short and broad, in male ending in globose terminalia (Figs. 7, 8), in female ending conically in soft unspecialized short ovipositor (Figs. 5, 6). Male terminalia (Steyskal 1957; Prado 1963, 1966) rather plesiomorphic, with tergite 6 free from syntergosternite 7 + 8 and accompanied by spiracles 6 and 7 in lateral membrane (Fig. 8); epandrium well-extended ventrally; surstylus well-developed, spatulate; cerci sometimes fused; hypandrium (Fig. 7) U-shaped; gonopod reduced to broad low blade; paramere well-developed, with one to three lobes; aedeagus rather short and simple, with well-developed spur-like epiphallus at posterior base; aedeagal apodeme short and spatulate; sperm pump small, with spatulate ejaculatory apodeme. Female with two sclerotized spermathecae; these ovoid, fusiform, or sausage-shaped, usually with distinct peduncle; one spermatheca sometimes partially or wholly duplicated.

Biology and behavior. Prado (1966) gave a resumé of the bionomics of Ropalomeridae, citing rearings from a gummy secretion of *Enterolobium timbouva*, presumably from wood of *Cocos nucifera*, from resin of *Spondias lutea*, and from a stump of a species of *Musa*. Aldrich (1932), in his description of *Rhytidops floridensis* (Aldrich), stated that adults were reared from decayed wood of *Sabal palmetto* and *S. minor*, but he described no immature forms, and apparently no specimens of them were preserved. The only morphological data concerning larvae are those of Lopes (1932), pertaining to *Ropalomera stictica* Wiedemann. The puparium of *Willistoniella pleuropunctata* (Wiedemann) was described by Fischer (1932), and that of *Ropalomera clavipes* (Fabricius) was figured by Lopes (1932). The posterior spiracles are medially contiguous in the larvae and puparia, and have three similar parallel and horizontal slits in each. Eggs of *Willistoniella pleuropunctata* were dissected from the female by Prado (1966) and described as similar to those of *Ropalomera stictica* illustrated by Lopes (1932).

Classification and distribution. The family Ropalomeridae is restricted to tropical and subtropical America and includes about 30 species, only one of which, *Rhytidops floridensis*, has been found north of Mexico.

The family was first revised by Lindner (1930), and more recently by Prado (1963, 1966). It was cataloged by Steyskal (1967). The only Nearctic species, *Rhytidops floridensis*, was placed in that genus by Malloch (1941), who also gave a key to genera. Three additional species, *Mexicoa mexicana* Steyskal, *Ropalomera femorata* (Fabricius), and *Willistoniella pleuropunctata*, may eventually be found in the southernmost United States and are therefore included in this treatment.

Key to genera

1. Arista practically bare (Fig. 3). Scutellum broader than long .... ***Rhytidops*** Lindner

   1 sp., *floridensis* (Aldrich); Florida; Aldrich 1932

   Arista distinctly plumose (Figs. 2, 4). Scutellum sometimes longer than broad 2

2. Scutellum longer than broad, with shallowly concave dorsal channel (Fig. 1). Arista with long dorsal and ventral rays. Posterior spiracle with a single bristle .... ***Ropalomera*** Wiedemann

   16 spp.; Neotropical, but 1 sp., *femorata* (Fabricius), may eventually reach southernmost U.S.A.; Prado 1966

   Scutellum broader than long, flat or convex dorsally. Arista with long dorsal and ventral rays (Fig. 4) or with flattened hairs all around (Fig. 2). Posterior spiracle with two or more bristly setae 3

3. Arista with long dorsal and ventral rays (Fig. 4). Facial protuberance developed as vertical ridge, ending in hump between bases of antennae (Fig. 4) .... ***Willistoniella*** Mik

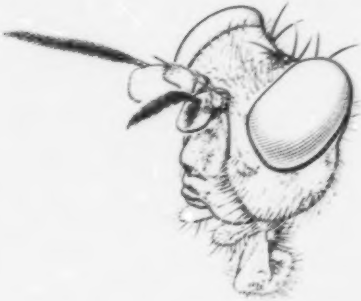
   1 sp., *pleuropunctata* (Wiedemann); Neotropical, not yet found north of Mexico; Prado 1963

   Arista furnished on all sides with flattened hairs (Fig. 2). Facial protuberance a small roundish hump below lower margin of eyes (Fig. 4) .... ***Mexicoa*** Steyskal

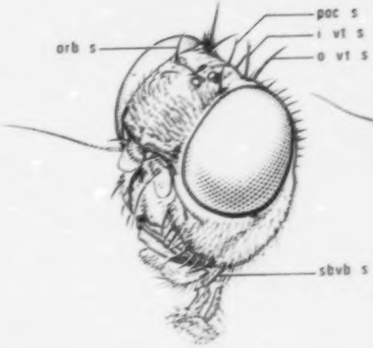
   1 sp., *mexicana* Steyskal; Neotropical, not yet found north of Mexico; Steyskal 1947

Figs. 85.2–8. Heads and terminalia: heads of (2) *Mexicoa mexicana* Steyskal (Neotropical), (3) *Rhytidops floridensis* (Aldrich), and (4) *Willistoniella pleuropunctata* (Wiedemann) (Neotropical); (5) left lateral and (6) ventral views of female terminalia of *W. pleuropunctata*; (7) ventral and (8) left lateral views of male terminalia of *W. pleuropunctata*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hypd apod, hypandrial apodeme; hyprct, hypoproct; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; st, sternite; sbvb s, subvibrissal seta; sur, surstylus; syntgst, syntergosternite; tg, tergite.



2 Mexicoa mexicana ♀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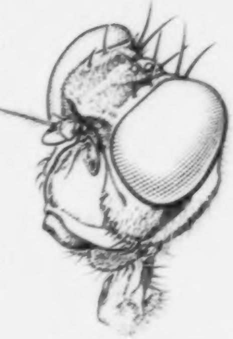
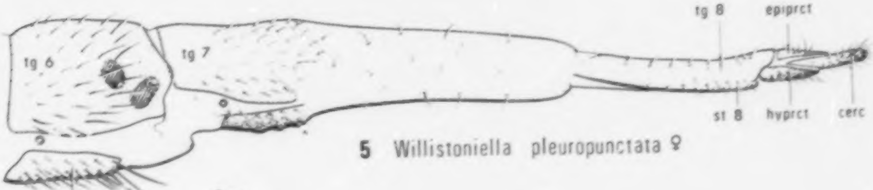
3 Rhytidops floridensis ♂



4 Willistoniella pleuropunctata ♀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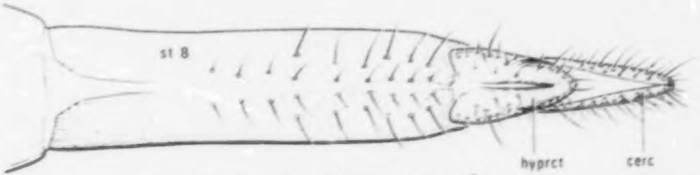
5 Willistoniella pleuropunctata ♀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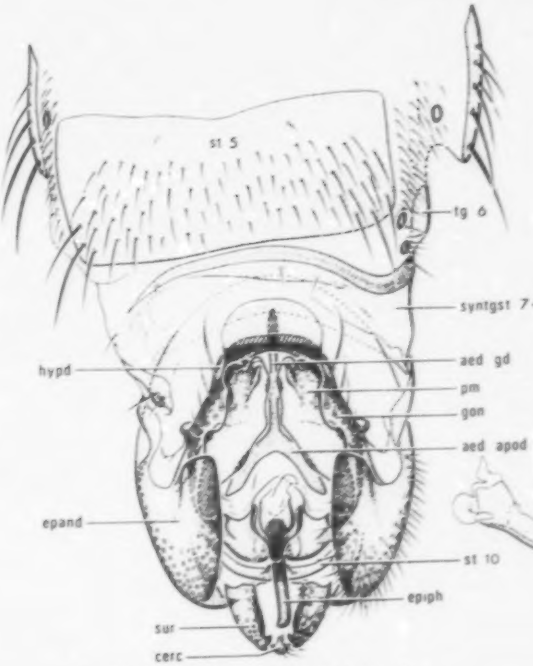
6 Willistoniella pleuropunctata ♀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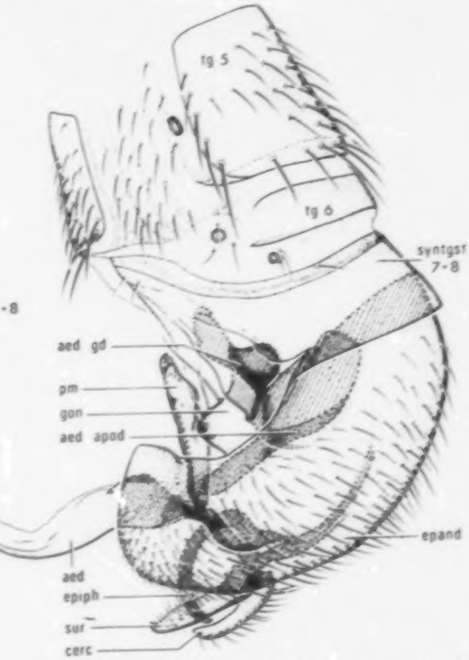
7 Willistoniella pleuropunctata ♂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8 Willistoniella pleuropunctata ♂

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SEPSIDAE

86

GEORGE C. STEYSKAL

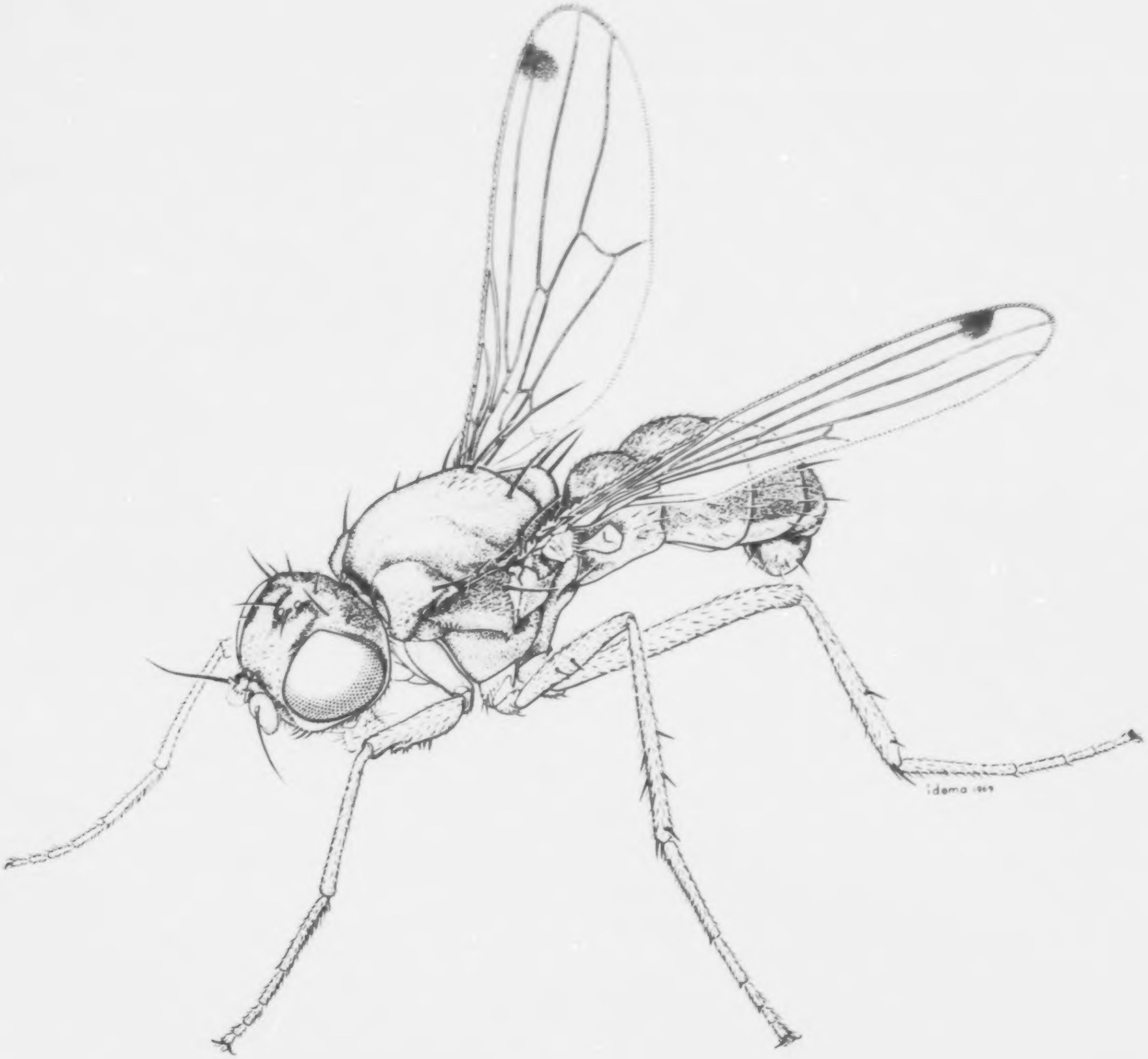


Fig. 86.1. Adult male of *Sepsis punctum* (Linnaeus).

Rather slender flies of medium size (Fig. 1), 2–6 mm long, usually dark metallic purplish, but sometimes dull black, or brownish to yellowish. Wing hyaline, usually with a dark spot near its tip.

Adult. Head: more or less globular (Figs. 2–5). Eye moderately large. Antenna short; arista bare. Palpus short to rudimentary. Chaetotaxy somewhat reduced; ocellar bristles and inner vertical bristles always present; outer vertical bristle present (Figs. 2, 3) or absent (Figs. 4, 5); one to three orbital bristles present.

Thorax: of ordinary proportions (Figs. 1, 6), usually mostly shining, but sometimes quite dull dorsally; silvery pruinescence present on pleuron, modified in extent, taxonomically significant. Chaetotaxy: one or two dorsocentral, zero or one postpronotal, two notopleural, one postsutural supra-alar, one strong proepisternal, zero or one proepimeral, one katepisternal, and one or two scutellar bristles present; anterior scutellar bristle usually quite small. Posterior spiracle with one or more distinct setae present on posteroventral margin (Fig. 6); this characteristic distinguishing this family from all North American acalyptrate families except Ropalomeridae and some Richardiidae.

Wing (Figs. 13, 14) usually rather narrow, hyaline or rarely milky, often with dark spot at tip of R_{2+3} (Sepsini), and sometimes blackish at extreme base. Venation varying little from types figured.

Legs (Figs. 7–12) rather slender. Fore femur and often fore tibia of male with specializations in form of bristles, tubercles, or emarginations (Figs. 7–10) for grasping base of wings of female during copulation. Middle tarsus of male sometimes with enlarged or varicolored segments (Fig. 11). Hind tibia of male, especially in *Themira* Robineau-Desvoidy and related genera, often furnished with a slit or elongated area known as an osmeterium (Fig. 12).

Abdomen: rather slender (Figs. 15–17), sometimes with prebasal constriction giving fly an ant-like appearance (Fig. 1). Female terminalia (Fig. 17) rather short and of generalized structure. Male with complex, often asymmetric, terminalia bearing forcipate surstyli (Figs. 15, 16, 18, 19); abdominal sternite 4 highly specialized, often bearing tubercles, processes, or long hair-tufts (Figs. 15, 16).

Larva. Typically maggot-like (Fig. 20), distinguished from other acalyptrate larvae by a somewhat bulbous more or less spiculate posterior end. Anterior spiracles more or less dendritic, usually with distinctly elongated median axis. Posterior spiracles on basally contiguous spiracular plates at end of short constriction at posterior end of body; this constriction also usually bearing accessory processes. Immature stages of many North American species not described, but descriptions of several of the Holarctic species provided by Hennig (1949) and Mangan (1977).

Biology and behavior. The Sepsidae are most often found on dung, but some species are found at decaying animal and vegetable matter, some at flowers, and some apparently in connection with ants. When walking about, these flies repeatedly flip their wings outward.

Classification and distribution. The family is of worldwide distribution, with many species found on more than one continent. Two subfamilies, Orygmatinae and Sepsinae, are recognized here. The subfamily Orygmatinae contains only one Holarctic genus and species, *Orygma luctuosum* Meigen, but several tribes are recognized in the Sepsinae. The tribes Saltellini and the Sepsini are represented in the Americas; the third tribe, the Toxopodini, is restricted to the southern parts of the Old World. The tribe Saltellini includes only the genus *Saltella* Robineau-Desvoidy; the tribe Sepsini is represented by 10 genera in the Nearctic region.

Because of the broad distribution of many species, the account of the Palaearctic species by Hennig (1949) contains a wealth of information pertinent to our fauna. The only comprehensive treatments of the North American species are by Melander and Spuler (1917) and Duda (1926). Specific diagnostic characters are found mainly in the male and include characters of the terminalia and secondary sexual modifications of the legs. The female is often difficult to determine.

The following key includes all genera known to occur in the Americas; only one genus, *Meropliosepsis* Duda, is not known to occur north of Mexico.

Key to genera

1. Frons with three strong orbital bristles (Fig. 2). Scutellum uniformly coarsely setose (Fig. 6). Robust nonmetallic bristly flies with strong setae on legs and abdomen ....ORYGMATINAE....***Orygma*** Meigen

1 sp., *luctuosum* Meigen; Atlantic coast from Massachusetts and northward, Europe

Frons with one or no strong orbital bristles. Disc of scutellum bare (Fig. 1). Rather slender usually metallic blackish flies, with few or no strong setae on legs and abdomen (Fig. 1) ....SEPSINAE....2

2. Scutellum strongly flattened, nearly as long as wide. Cells br and bm united (Fig. 14) ....SALTELLINI....***Saltella*** Robineau-Desvoidy

1 sp., *sphondylii* (Schrank); Holarctic

Scutellum convex, not or scarcely half as long as wide. Cells br and bm separated (Fig. 13) ....SEPSINI....3

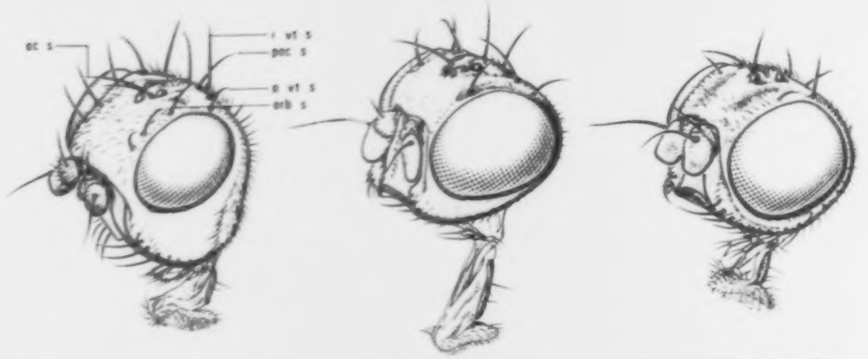
3. Anepisternal bristle and outer vertical bristle absent (Figs. 4, 5). Male with broadened (not linear) osmeterium on hind tibia (Fig. 12) 4

Anepisternal bristle (as in Fig. 6) and sometimes outer vertical bristle present (as in Figs. 2, 3). Male with or without osmeterium on hind tibia; if present, linear 6

4. Postpronotal bristle long and strong (as in Fig. 6) ....***Themira*** Robineau-Desvoidy

9 spp.; widespread northward; Mangan 1976

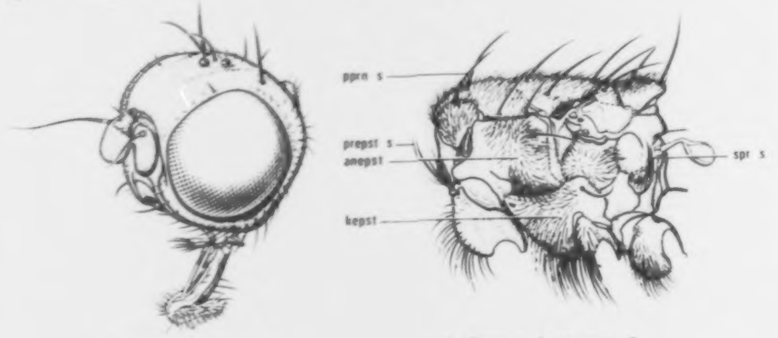
Postpronotal bristle absent 5



2 Orygma luctuosum ♂

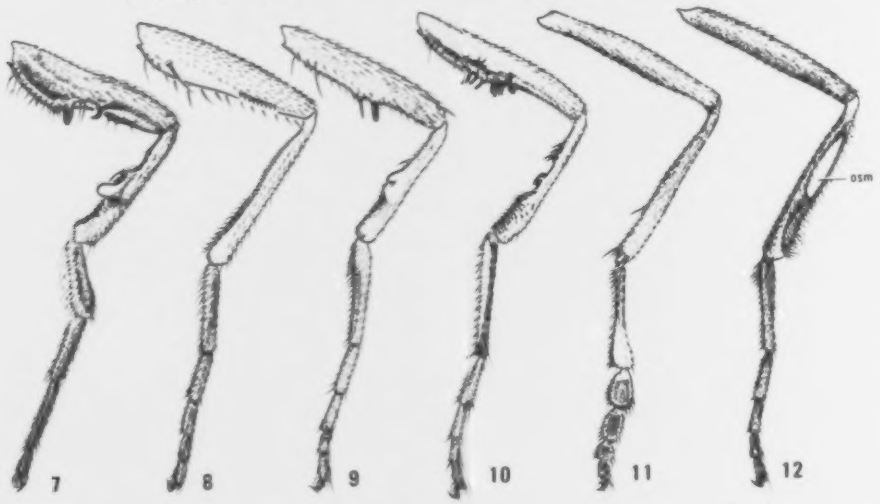
3 Saltella sphondylii ♂

4 Enicomira minor ♂



5 Enicita annulipes ♂

6 Orygma luctuosum ♂



7 Themira putris ♂

8 Nemopoda nitidula ♂

9 Meroplius stercorarius ♂

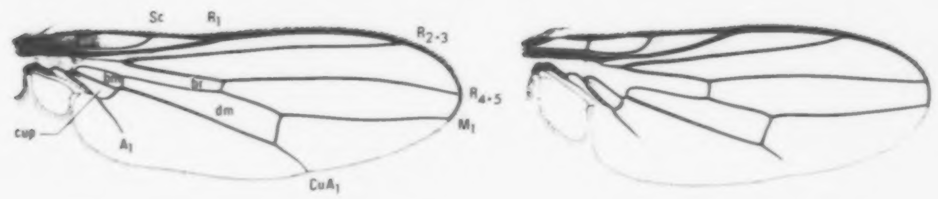
10 Decachaetophora aeneipes ♂

11 Enicita annulipes ♂

12 Themira putris ♂

Figs. 86.2–12. Details of head, thorax, and legs: heads of (2) *Orygma luctuosum* Meigen, (3) *Saltella sphondylii* (Schrank), (4) *Enicomira minor* (Haliday), and (5) *Enicita annulipes* (Meigen); (6) thorax of *Orygma luctuosum*, left lateral view; anterior views of left front leg of male of (7) *Themira putris* (Linnaeus), (8) *Nemopoda nitidula* (Fallén), (9) *Meroplius stercorarius* (Robineau-Desvoidy), and (10) *Decachaetophora aeneipes* (Meijere); anterior views of (11) midleg of male of *Enicita annulipes* and (12) of left hindleg of male of *Themira putris*.

Abbreviations: anepst, anepisternum; i vt s, inner vertical seta; kepst, katepisternum; oc s, ocellar seta; orb s, orbital seta; osm, osmeterium; o vt s, outer vertical seta; poc s, postocellar seta; pprn s, postpronotal seta; prepst s, proepisternal seta; spr s, spiracular seta.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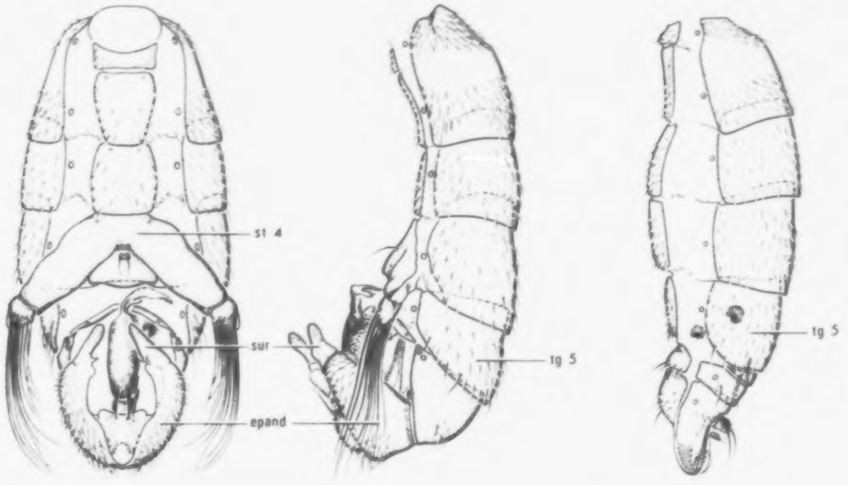
13 Decachaetophora aeneipes ♂ **14** Saltella sphondylii ♂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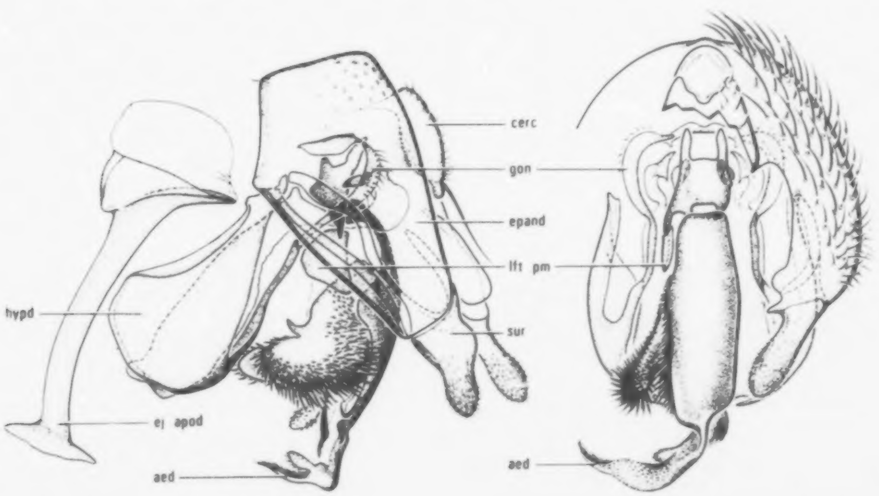
15 Themira putris ♂ **16** Themira putris ♂ **17** Themira putris ♀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18 Themira putris ♂ **19** Themira putris ♂

Figs. 86.13–19. Details of wing and abdomen: wings of (13) *Decachaetophora aeneipes* (Meijere) and (14) *Saltella sphondylii* (Schrank); (15) ventral and (16) left lateral views of male abdomen of *Themira putris* (Linnaeus); (17) female abdomen of *Themira putris*, left lateral view; (18) left lateral and (19) posteroventral views of male terminalia of *Themira putris*.

Abbreviations: aed, aedeagus; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; lft pm, left paramere; st, sternite; sur, surstylus; tg, tergite.

5. Head longer than high; postocellar bristles minute and close together, less than half as long as ocellar bristles (Fig. 5). Postpronotal lobe and scutum entirely uniformly pruinose. Fringe of calypter brownish. Male with expanded tarsomeres on midleg (Fig. 11) .... ***Enicita*** Westwood

2 spp.; 1 Holarctic sp. in eastern Canada and U.S.A., 1 Nearctic sp. in Texas

Head not longer than high; postocellar bristles strong and widely separated, more than half as long as ocellar bristles (Fig. 4). Postpronotal lobes and lateral portions of scutum polished. Fringe of calypter white. Male without expanded tarsomeres on midleg .... ***Enicomira*** Duda

1 sp., *minor* (Haliday); widespread Holarctic southward to northern U.S.A.

6. Wing without dark spot at end of R_{2+3}. Katepisternum silvery pruinose only on upper border. Presutural dorsocentral bristles absent 7

Wing with dark spot at end of R_{2+3}. Katepisternum usually entirely silvery pruinose; if not (*Meropliosepsis*), then scutum with one pair of presutural dorsocentral bristles 10

7. Postpronotal bristle absent .... ***Decachaetophora*** Duda

1 sp., *aeneipes* (Meijere); immigrant in northwestern U.S.A. and British Columbia, from Asia; Steyskal 1943

Postpronotal bristle present (as in Fig. 6) 8

8. Scutum with two pairs of postsutural dorsocentral bristles. Orbital bristle absent .... ***Palaeosepsis*** Duda

2 spp.; Texas and Florida (several other species south of U.S.A.)

Scutum with one pair of postsutural dorsocentral bristles. Orbital bristle present, though sometimes minute 9

9. Orbital bristle minute, one-quarter as long and strong as postocellar bristles. Fore femur of both sexes with a close series of 6–10 small spinules near apex of anteroventral surface (Fig. 8) .... ***Nemopoda*** Robineau-Desvoidy

1 sp., *nitidula* (Fallén); Holarctic, mostly northward (three other dubious spp.)

Orbital bristle strong, nearly as long and strong as postocellar bristles. Fore femur without a close series of small spinules, though male (Fig. 9) has several stout bristles and female has one bristle in this position .... ***Meroplius*** Rondani

1 sp., *stercorarius* (Robineau-Desvoidy); widespread in Holarctic

10. Scutum with one presutural and two postsutural pairs of dorsocentral bristles. Body almost entirely pale brownish .... ***Meropliosepsis*** Duda

1 sp., *sexsetosa* Duda; Central and South America

Scutum without presutural dorsocentral bristles. Body usually mostly blackish 11

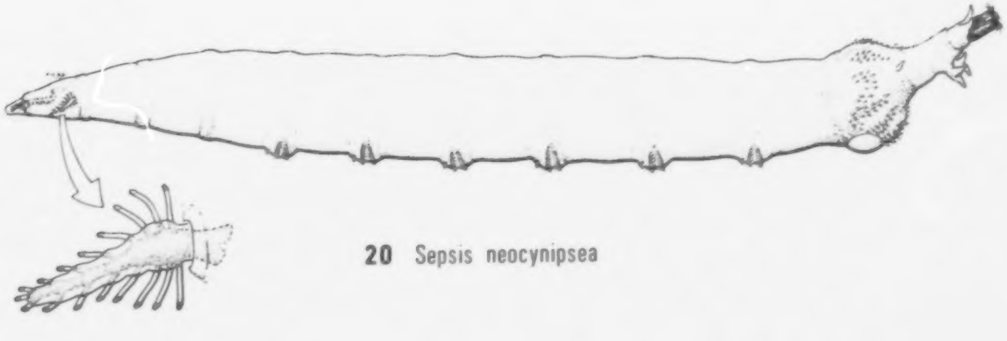

Fig. 86.20. Larva of *Sepsis neocynipsea* Melander & Spuler.

11. Lateral setae of second abdominal tergite not longer and stronger than on following tergites. Male fore femur without tubercle .... ***Sepsidimorpha*** Frey

3 spp.; widespread but scarce

Lateral setae of second abdominal tergite longer and stronger than on following tergites. Male fore femur with distinct tubercle below .... ***Sepsis*** Fallén

6 recognized spp.; mostly Holarctic

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LAUXANIIDAE

87

G. E. Shewell

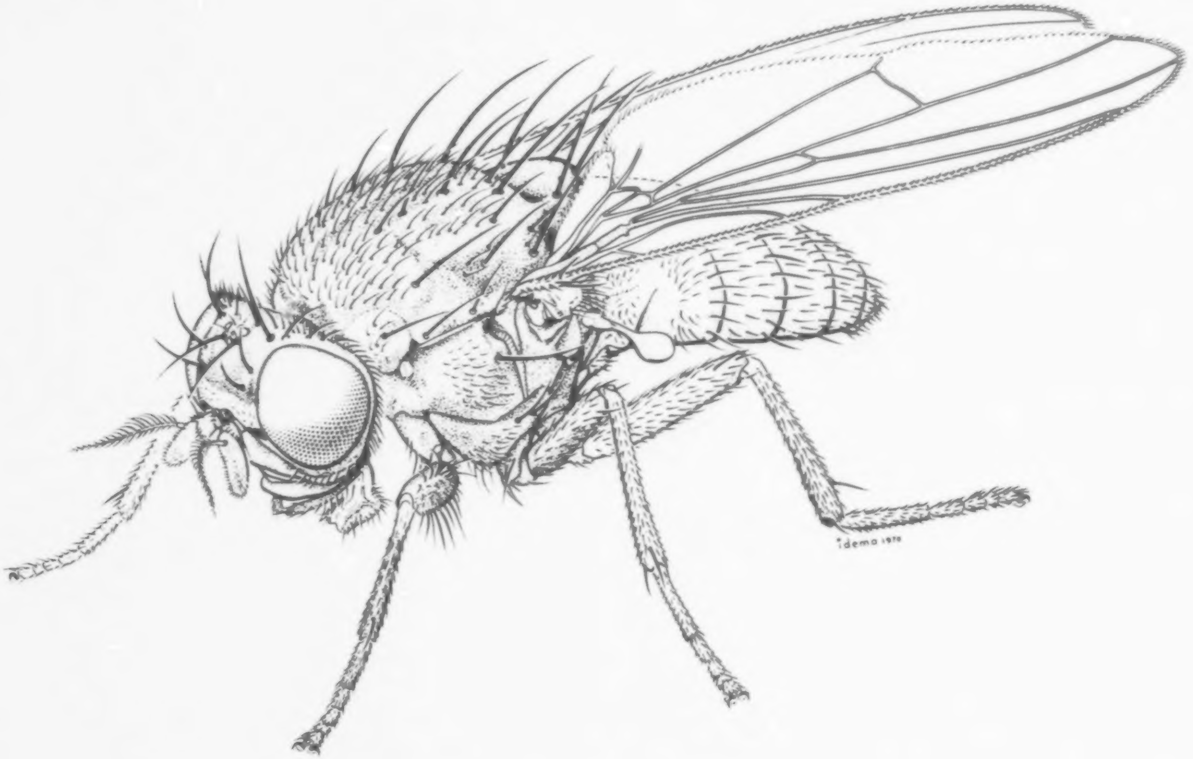


Fig. 87.1. Male of *Minettia lupulina* (Fabricius).

Small usually robust flies (Fig. 1), 2.5–5.5 mm long, dull or polished, yellow, brown, gray, black, or combinations of these, sometimes with dark spots or vittae. Wing often yellow-tinged, sometimes spotted or clouded. Sexes similar; male dichoptic, sometimes with sexual modification of abdominal sternites and hindleg (Figs. 52, 53); terminalia in both sexes variable in size and complexity.

Adult. Head: usually nearly twice as wide as long (Figs. 14, 15, 17–19), in profile more or less oval, higher than long (Figs. 2–6, 8, 9, 11–13), rarely elongate triangular with produced frons and strongly retreating face (Figs. 7, 10). Frons subquadrate, seldom much longer than wide (Figs. 41–43), flat or convex, more or less haired anteriorly, forming angle with face or else strongly sloped and merging into facial plane; orbital plates usually evident. Two pairs of orbital setae usually reclinate, evenly spaced in line between inner vertical setae and antennae, sometimes with the anterior pair more or less convergent; ocellar setae hair-like or strong, divergent or parallel; postocellar setae convergent and cruciate. Vertex rounded or carinate; inner and outer vertical setae strong. Face about as long as frons, flat or bulging, sometimes carinate above, seldom concave; frontogenal suture usually present, often reaching base of antenna (Figs. 44–46). Parafacial mostly bare, about one-fourth to over half facial width, seldom greatly narrowed below, with a row of fine setae or hairs below continuous with subvibrissal series; uppermost seta occasionally stronger (Figs. 35, 44, 45). Eye oval, usually higher than long, bare or sparsely micropubescent, sometimes slightly concave in outline posteroventrally (Figs. 1, 2, 11). Gena about one-sixth height of eye, seldom broader, bare except along subgenal suture; vibrissae absent; subgena narrow; clypeus sometimes slightly projecting; postgena haired and usually with two genal bristles. Occiput above foramen more or less concave, bare except for a patch of supracervical setae. Antennae adjacent or well-separated, usually short, with scape bare below and first flagellomere round or short oval, about 2.5 times longer than wide; sometimes all segments elongate, in which case scape often with ventral hairs and first flagellomere tapering or cylindrical and up to eight times longer than wide (Figs. 13, 16); arista bare to long plumose. Proboscis short; labella fleshy; palpus narrowly clavate.

Thorax: scutum moderately convex (Figs. 1, 31, 47–49). Scutellum about one-third length of scutum, convex or somewhat flattened; prescutellum absent; rudimentary subscutellum present. Chaetotaxy: dorsocentral setae in arrangements of 1+3, 1+2, 0+3, or 0+2, usually all strong and evenly spaced; occasionally postsutural series decreasing in length anteriorly, in which case presutural pair absent; acrostichal hairs in 2–10 rows; acrostichal setae, except prescutellar pair, seldom present (Figs. 47–49); intra-alar setae usually absent; sometimes a postsutural intra-alar seta present midway between supra-alar and posterior dorsocentral setae (Fig. 31); one presutural supra-alar seta usually present; one postsutural supra-alar seta and two postalar setae present; one basal and one apical scutellar seta present; very rarely a few scutellar hairs present laterally; one postpronotal and two notopleural setae present, the posterior notopleural weaker; one proepisternal seta present, sometimes weak; proepimeral seta absent; middle of propleuron bare; one anepisternal seta present; two katepisternal setae present, the anterior one sometimes weak or absent. Anepimeron (pteropleuron) usually bare, rarely with one to three fine hairs above. Prosternum bare or sparsely haired.

Wing with length-to-width ratio about 2.3:1, rarely 2:1. C unbroken, weakened beyond R_{4+5}, ending at M_1 (Figs. 20, 21); anterodorsal surface with stout black spinules from beyond humeral crossvein to beyond apex of R_{2+3}, sometimes continued to apex of R_{4+5}; anteroventral surface with row of numerous hairs extending to beyond wing apex; ventral surface usually with very sparse row of inconspicuous hairs to about apex of R_{2+3}; sometimes these hairs numerous and conspicuous, especially toward base of wing (Figs. 56, 57). Sc complete, separated from R_1. Basal part of Rs sometimes with one or two fine hairs on upper side (Fig. 23). Crossvein r-m at about middle of cell dm, seldom much beyond; sometimes a crossvein present between R_{4+5} and M beyond crossvein dm-cu (Figs. 24, 26). Cell cu*p* small, with apex rounded. A_1 ending abruptly far from wing margin.

Legs (Figs. 27–30, 52–54) usually with preapical dorsal seta on all tibiae (Figs. 52–54), but this sometimes absent from hind tibia. Fore femur sometimes with anteroventral ctenidium near apex (Fig. 29) and with rows of five or six posterodorsal, posteroventral, and posterior setae, although the latter row is sometimes incomplete; mid femur with row of three or four anterior setae on apical half, rarely reduced or absent. Mid tibia with one to three apical spurs (Figs. 27, 28), rarely with row of short posterior setae (Fig. 54); claw of mid tarsus occasionally modified in male. Hind femur with preapical anterodorsal seta, sometimes also with preapical anteroventral and posteroventral setae in female, or anteroventral and posteroventral rows in male; hind tibia sometimes with long anteroventral and posteroventral hairs in male; hind tarsus sometimes ornamented (Figs. 52, 53).

Abdomen: usually short ovoid, wider than deep, rarely slender, parallel-sided or tapered; six segments preceding terminalia; two visible genital segments in the male and three in the female. Sternites small, usually wider than long; sternite 1 sometimes with basal margin invaginated; sternite 2 with a supplementary, very short, bare, polished sclerite narrowly separated from its basal margin; male sternites 2–5 sometimes variously modified. Pleural membrane bare and smooth or with rugose setigerous areas, occasionally with prominent eversible sacs in female. Spiracles 1–5 very small, set in membrane just below tergites; spiracle 6 sometimes and spiracle 7 often situated in wall of corresponding tergite far from its margin.

Female oviparous. Terminalia (Figs. 61, 63, 65) long and tapering or short and blunt. Segment 7 usually little modified, sometimes forming complete sclerotized ring. Tergite 8 small; sternite 8 more or less strongly sclerotized, frequently enlarged. Epiproct very small, scutate; hypoproct usually small, micropilose, with softly rounded apex, sometimes rigidly sclerotized and forming egg guide with sternite 8. Cercus small, papillate. Three sclerotized spermathecae present (Figs. 61, 63, 65).

Male with syntergosternite 7 + 8 usually small, sometimes large and strongly arched, often incomplete ventrally, usually enclosing spiracle 7. Epandrium (Figs. 58–60, 62, 64) small and hidden or large and projecting ventrally, sometimes with ventrolateral projections. Surstylus usually laminate or forcipate, occasionally complex and denticulate, either articulated or fused with epandrium. Hypandrium ring-shaped or trough-like, with or without median or sublateral projections, and sometimes divided midventrally; gonopod often absent, rarely well-developed; paramere usually present, often complex and massive; aedeagus usually with internal or external stylets or teeth of varying size, seldom entirely membranous; aedeagal apodeme freely articulated, usually shorter than aedeagus; ejaculatory apodeme very small. Sternite 10 (visible only in cleared material) usually present, weakly sclerotized, joining surstyli as a narrow bridge between their bases. Cercus usually short papillate, sometimes greatly enlarged and spatulate (Fig. 59).

Egg. Length 0.58–0.84 mm, width 0.16–0.32 mm, white, ovoid, sometimes flattened dorsally. Ends usually tuberculate, with reticulated surface and with micropyle beneath anterior tubercle. Chorion with 5–30 longitudinal ridges sometimes connected by transverse septa or bearing numerous prominent spicules.

Larva. White or colorless, more or less translucent, cylindroconical, somewhat compressed dorsoventrally (Fig. 66). All segments with anterodorsal spinule-bands, and segments 3–12 with anteroventral spinule-bands. Segment 1 bilobate; antenna short, two-segmented; maxillary palpus lacking sclerotized basal ring; facial mask with rows of spicules. Cephalopharyngeal skeleton (Figs. 70, 71) with paired mandibles. Anterior spiracle with dendriform or flabelliform filaments on short stalk (Fig. 67). Terminal segment with ventral anal pad bearing extrusible lateral lobes (Fig. 68). Spiracular disc usually with four marginal tubercles; spiracular plates mounted on short tubes near dorsal margin of disc, each with four multibranched spiracular hairs (Figs. 68, 69).

First instar (Fig. 71) metapneustic, 0.72–2.01 mm long. Cephalopharyngeal skeleton 0.18–0.30 mm long; mandible with long slender basal part, without clear spot; apical part of mandible usually with subbasal tooth plus accessory tooth beside or behind main hook; rarely entire structure weak. Dental sclerite lacking; epipharyngeal and hypopharyngeal sclerites apparently fused, latter with weak bridge and with posteroventral margin joined to tentoropharyngeal sclerite. Parastomal bars lacking. Floor of tentoropharyngeal sclerite weakly developed.

Second instar 1.40–4.36 m long and 0.35–0.91 mm wide, similar to third instar but usually with only one accessory tooth on mandible. Hypopharyngeal and tentoropharyngeal sclerites fused; floor of latter with fewer ridges. Head of anterior spiracle with nodular branches in flabelliform type and unbranched in dendriform type.

Third instar 2.91–7.14 mm long and 0.56–1.75 mm wide. Mandible usually strong, convergent in dorsal view, strongly curved with sharp apex in profile. Dental, labial, and epipharyngeal sclerites, as well as parastomal bars, usually all present; hypopharyngeal sclerite with long narrow bridge and slender arms, of which the anterior pair is truncate; labial sclerite arched, with slender posterior rami medial to parastomal bars; tentoropharyngeal sclerite with nine ridges in floor; dorsal bridge usually broad, sometimes with clusters of oval transparent areas; dorsal cornu shorter and narrower than ventral cornu; latter often with elongate transparent area on upper margin. Anterior spiracle (Fig. 67) either with long stalk and flabelliform head bearing five to nine branches or with short stalk and multi-branched dendriform head. Posterior spiracular plate circular; slits short oval with pigmented rims, evenly spaced, radiating outward; spiracular hairs each with 6–20 branches; a small oval ecdysial scar present near inner margin (Fig. 69).

Puparium. Ovoid, convex dorsally, flattened ventrally; segmentation defined by lateral convexities. Surface usually covered with calcareous deposit expelled as liquid from larval anus at pupation.

Biology and behavior. Miller and Foote (1975, 1976) have given extensive biological data on the Nearctic species. Malloch (1927) described and illustrated puparia of two of these. In Europe, rearing records of several species from leaf litter, dead thistle heads, rotting tree stumps, and even cow dung have been published, mostly without illustration, but no precise studies have been undertaken. Descriptions of immature stages given in the preceding paragraphs are based on the work of Miller and Foote cited above. Eight species in seven genera were studied, six breeding in leaf or other plant litter and two in bird's nests. Because of the difficulty of finding immature stages in the field, data were obtained by inducing oviposition under laboratory conditions and by rearing larvae on a variety of decaying plant material, including lettuce leaves.

In leaf litter species, field-caught adults survive about 80 days under controlled conditions. Females from the field lay on average 250 eggs, either singly or in small clusters at a daily rate of 1–10 eggs. Oviposition takes place in late afternoon and evening. In some species, the incubation period is variable apparently because some eggs were in weak diapause; thus the egg stage may last from 3 days to several months. Diapause may sometimes be broken by lowering the temperature to 5–7°C. The first instar larva feeds between the epidermal layers, but later stages may feed externally between adjacent leaves. There is some indication of specific host plant association, since larvae, when given a choice, prefer leaves of *Acer* and *Prunus* and fail to reach maturity in *Populus*, *Salix*, *Alnus*, or *Ulmus*. Leaves of *Quercus* and *Fagus* are rejected. There seems little doubt that larval food consists of microorganisms or fungi, or both, associated with decay in various plant species. The larval period varies from 10 days to more than 2 months, the pupal period being 2 weeks or less. Overwintering (at approximately 41°N lat) is in the larval or pupal stage. Adult lauxaniids in the field are sedentary and shade loving. They may be collected by sweeping low foliage and undergrowth, especially in damp woods and near streams and marshes. In general, they appear not to be anthophilous, but data on collectors' labels indicate that some genera occur on flowers in large numbers. They have also been taken in traps baited for Drosophilidae or Sarcophagidae and are sometimes attracted to artificial light. Miller (1977*b*) has summarized the ecological literature on the family and has given a complete bibliography.

Classification and distribution. Stuckenberg (1971) proposed a subfamily Homoneurinae for about 19 genera that have the costal spinules continued to apex of R_{4+5}. All of these except *Homoneura* Wulp are confined to the Old World. Monophyly of this group is evident also from the presence of a ctenidium on the fore femur and of two (sometimes three) apical spurs on the mid tibia (Figs. 27, 29). Nearly all other genera lack a ctenidium and have a single spur (Figs. 28, 30). The small number of genera involved (out of a total of over 150) and the relative scarcity of the group in the New World suggest that tribal status might be more appropriate. In any case, there is still difficulty in recognizing further higher groups among the remaining genera although several possibilities are available based on *Minettia* Robineau-Desvoidy, *Trigonometopus* Macquart, and a few others. Among the genera that, like *Lauxania* Latreille, have the antenna elongate cylindrical, parallel evolution has clearly occurred. A tribal division therefore could not be based primarily on this character. *Sapromyza* Fallén in its present state may be compared to *Sarcophaga* Meigen of a few years ago. Redefinition and recognition of its many species groups as distinct genera or subgenera is overdue (Shewell 1986). Although many characters exist for defining genera in this family, the present state of knowledge is inadequate for providing a stable higher classification.

Lauxaniidae occur on all continents except Antarctica. They are specially plentiful in the tropics, and endemic species are found on many Pacific islands. In North America they occur up to the limit of trees. In their affinities, the described Nearctic species are about equally close to the Old World (75 spp.) and the New World (76 spp.), but at the generic level, the fauna is seen to belong much more to the New World, since only eight of the 30 genera or subgenera are Holarctic, and the large number of undescribed Nearctic species belongs almost exclusively to New World genera. Thus, 14 genera range more or less widely in Central and South America including the Caribbean, most of these having only one Nearctic representative. Seven genera are perhaps exclusively Nearctic, and two are pantropical or cosmopolitan. As pointed out by Stuckenberg (1971), the Neotropical fauna has little in common with that of the Old World.

Two lauxaniid genera have been described from Baltic amber (Hennig 1965), and a species of *Sapromyza* was described from Miocene shale in Colorado (Melander 1949). The type of *Lonchaea senescens* Scudder, a wing fragment from Tertiary deposits in British Columbia, has also been assigned to the Lauxaniidae (McAlpine 1962).

Key to genera

1. Anepimeron (pteropleuron) with one to several short fine hairs above 2

Anepimeron bare 4

2. Presutural dorsocentral seta absent. One katepisternal seta. Frons concave anteriorly in dorsal view. Anterior orbital seta slightly incurved, close to anterior margin of frons (Figs. 11, 14, 45) .... ***Neogriphoneura*** Malloch

1 sp., *sordida* (Wiedemann); southern U.S.A.

Presutural dorsocentral seta present. Two katepisternal setae. Anterior margin of frons not concave. Anterior orbital seta reclinate, not close to anterior margin of frons (Figs. 32, 36) 3

3. Face dull, flat (Fig. 36). Yellow to brownish yellow species .... ***Lyciella*** Collin

2 spp., including one immigrant; British Columbia to California

Face mostly polished, either concave or strongly convex (Fig. 32). Shining black species, sometimes with yellowish legs .... ***Calliopum*** Strand

5 spp.; British Columbia to California

4. C with black costal setulae extending to apex of R_{4+5} (Fig. 20). Mid tibia with two spurs (Fig. 27). Fore femur with ctenidium (Fig. 29). Head as in Fig. 46 .... ***Homoneura*** Wulp 5

Costal setulae ending well before apex of R_{4+5} (Fig. 21). Mid tibia with one spur (Fig. 28). Ctenidium usually absent (Fig. 30). Head various 6

5. Postocellar setae equal to or longer than ocellar setae, gradually convergent, their bases about as close together as posterior ocelli (Fig. 50). Usually at least one hind tarsal segment blackened (Figs. 52, 53) .... ***Homoneura*** (***Tarsohomoneura*** Hendel)

8 spp.; widespread; Miller 1977*a*

Postocellar setae usually shorter than ocellar setae, strongly convergent, their bases much farther apart than posterior ocelli (Fig. 51). Hind tarsal segments pale .... ***Homoneura*** (***Homoneura*** Wulp)

41 spp.; widespread; Miller 1977*a*

6. Anterior katepisternal seta absent or greatly reduced, hair-like 7

Anterior katepisternal seta shorter than posterior one but not hair-like 16

7. Dorsocentral setae arranged 0 + 3. Anterior orbital setae strongly convergent (inclinate) (Fig. 17). Yellow or brownish species 8

Dorsocentral setae arranged 0 + 2. Anterior orbitals reclinate (Fig. 18); if these more or less convergent, then black species 9

8. First flagellomere less than four times longer than wide, much shorter than arista. Face flat, rarely with median black spot (Fig. 33) .... ***Camptoprosopella*** Hendel

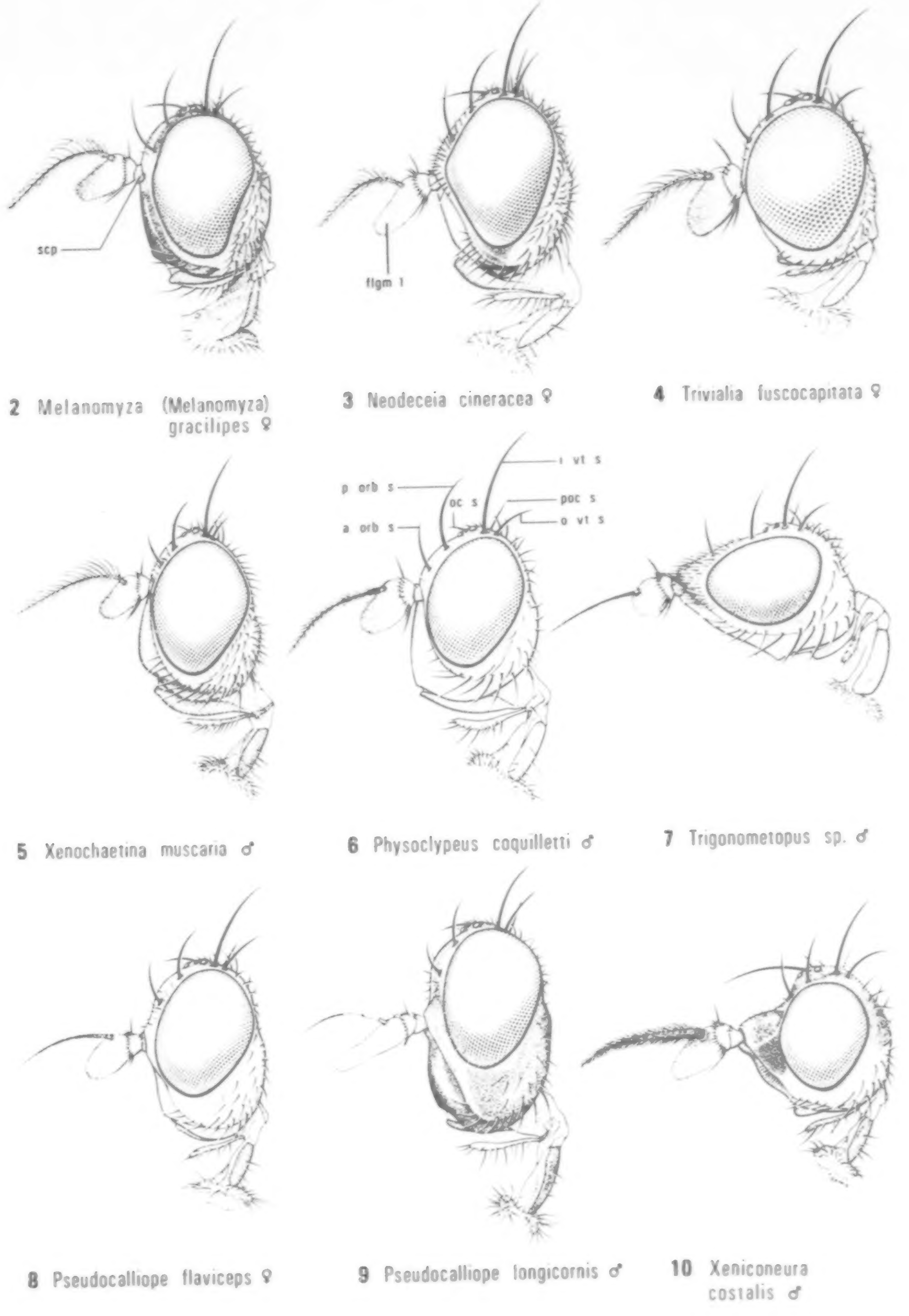
22 spp.; widespread; Shewell 1939

First flagellomere about eight times longer than wide, much longer than arista. Middle of face strongly tuberculate, with polished black spot (Fig. 34) .... ***Pachyopella*** Shewell

1 sp., possibly *flavida* (Wiedemann); Florida; Melander 1913 (as *Pachycerina*, in part)

9. Posterior dorsocentral seta as far from scutellum as anterior seta is from suture (Fig. 48) 10

Posterior dorsocentral seta much closer to scutellum than anterior one is to suture; rarely a reduced third postsutural seta present closer to suture (Fig. 49) 14



2 Melanomyza (Melanomyza) gracilipes ♀

3 Neodeceia cineracea ♀

4 Trivialia fuscocapitata ♀

5 Xenochaetina muscaria ♂

6 Physoclypeus coquilletti ♂

7 Trigonometopus sp. ♂

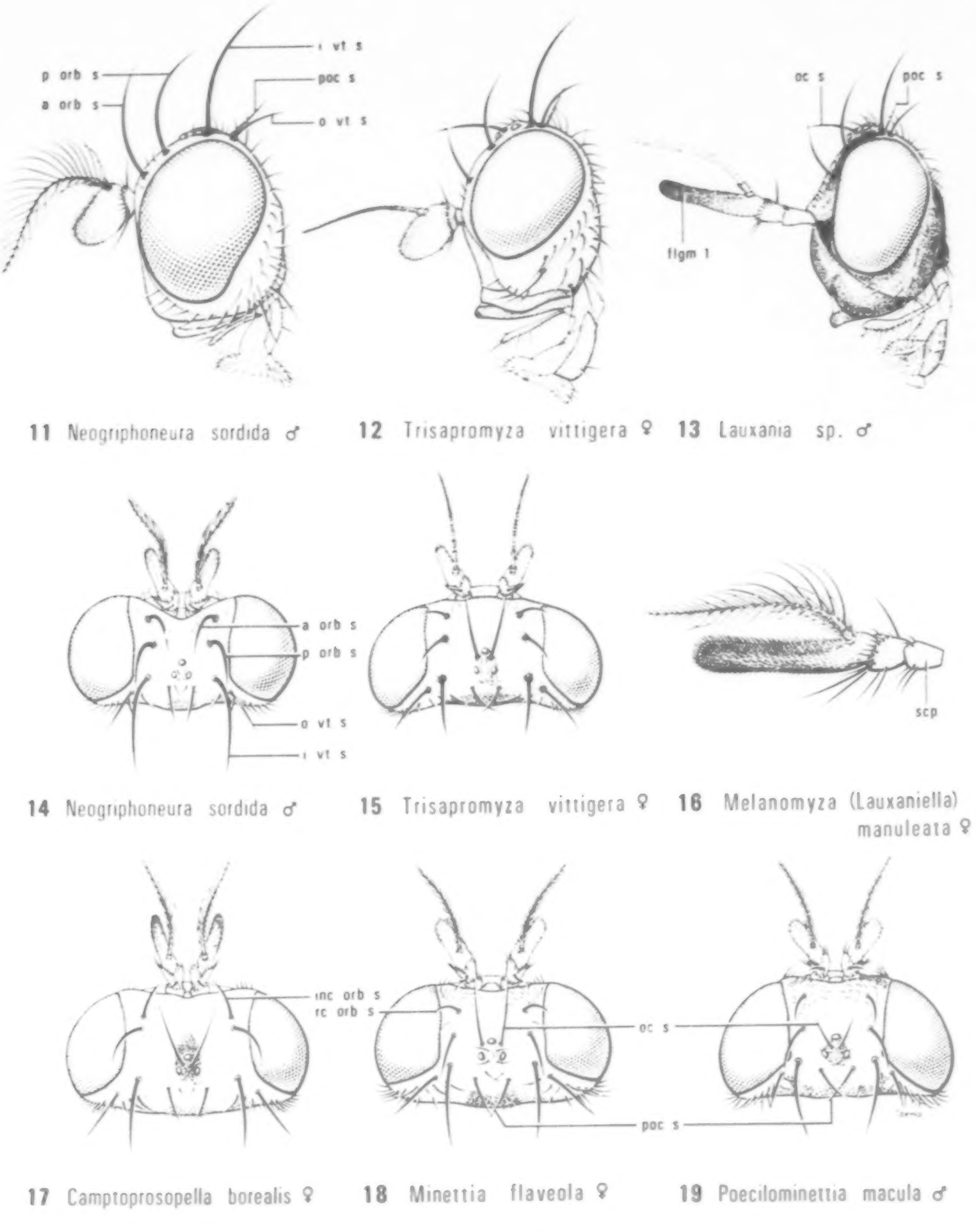
8 Pseudocalliope flaviceps ♀

9 Pseudocalliope longicornis ♂

10 Xeniconeura costalis ♂

Figs. 87.2–10. Lateral views of heads: (2) *Melanomyza (Melanomyza) gracilipes* (Loew); (3) *Neodeceia cineracea* (Coquillett); (4) *Trivialia fuscocapitata* (Malloch); (5) *Xenochaetina muscaria* (Loew); (6) *Physoclypeus coquilletti* (Hendel); (7) *Trigonometopus* sp.; (8) *Pseudocalliope flaviceps* (Loew); (9) *Pseudocalliope longicornis* (Coquillett); (10) *Xeniconeura costalis* (Curran) (*continued*).

Abbreviations: a orb s, anterior orbital seta; flgm, flagellomere; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; poc s, postocellar seta; p orb s, posterior orbital seta; scp, scape.



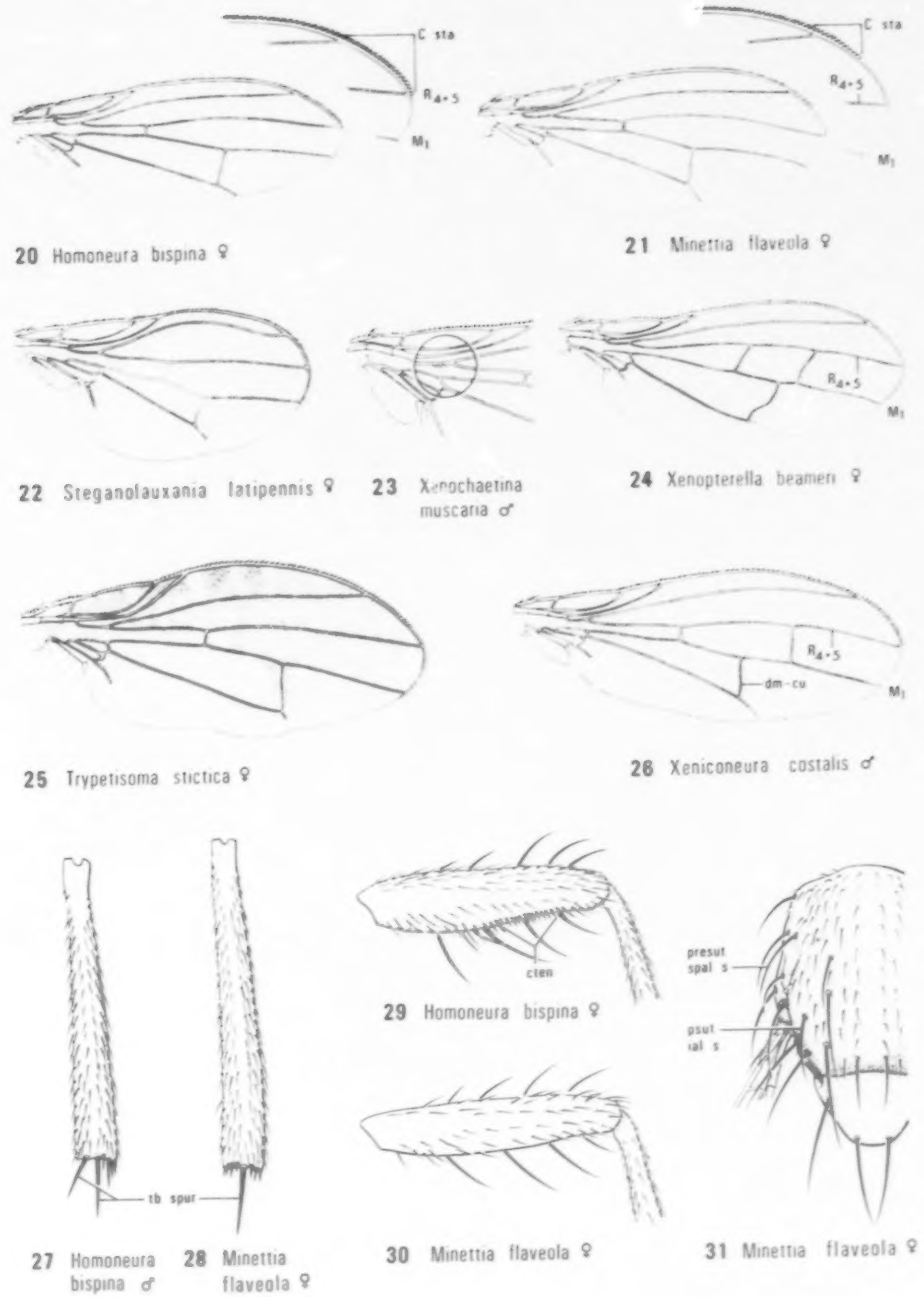
11 Neogriphoneura sordida ♂ **12** Trisapromyza vittigera ♀ **13** Lauxania sp. ♂

14 Neogriphoneura sordida ♂ **15** Trisapromyza vittigera ♀ **16** Melanomyza (Lauxaniella) manuleata ♀

17 Camptoprosopella borealis ♀ **18** Minettia flaveola ♀ **19** Poeciliominettia macula ♂

Figs. 87.11–19. Heads (*continued*) and antennae: lateral views of heads of (11) *Neogriphoneura sordida* (Wiedemann), (12) *Trisapromyza vittigera* (Coquillett), and (13) *Lauxania* sp.; dorsal views of heads of (14) *Neogriphoneura sordida* and (15) *Trisapromyza vittigera*; left antenna of (16) *Melanomyza* (*Lauxaniella*) *manuleata* (Loew); dorsal views of heads of (17) *Camptoprosopella borealis* (Shewell), (18) *Minettia flaveola* (Coquillett), and (19) *Poeciliominettia macula* (Loew).

Abbreviations: a orb s, anterior orbital seta; flgm, flagellomere; inc orb s, inclinate orbital seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; poc s, postocellar seta; p orb s, posterior orbital seta; rc orb s, reclinate orbital seta; scp, scape.


C sta
R4+5
M1
20 Homoneura bispina ♀
C sta
R4+5
M1
21 Minettia flaveola ♀
22 Steganolauxania latipennis ♀
23 Xenochaetina muscaria ♂
R4+5
M1
24 Xenopterella beameri ♀
25 Trypetisoma stictica ♀
R4+5
dm-cu
M1
26 Xeniconeura costalis ♂
tb spur
27 Homoneura bispina ♂
28 Minettia flaveola ♀
cten
29 Homoneura bispina ♀
30 Minettia flaveola ♀
presut spal s
psut ial s
31 Minettia flaveola ♀

Figs. 87.20–31. Wings, legs, and thorax: wings of (20) *Homoneura bispina* (Loew), (21) *Minettia flaveola* (Coquillett), and (22) *Steganolauxania latipennis* (Coquillett); (23) base of wing of *Xenochaetina muscaria* (Loew) showing (in circle) hairs on basal part of Rs; wings of (24) *Xenopterella beameri* Steyskal, (25) *Trypetisoma stictica* (Loew), and (26) *Xeniconeura costalis* (Curran); ventral views of left mid tibia of (27) *Homoneura bispina* and (28) *Minettia flaveola*; anterior views of left fore femora of (29) *Homoneura bispina* and (30) *Minettia flaveola*; (31) thoracic dorsum of *Minettia flaveola*.

Abbreviations: C sta, costal setula; cten, ctenidium; presut spal s, presutural supra-alar seta; psut ial s, postsutural intra-alar seta; tb spur, tibial spur.

10. Face convex, glossy (Fig. 2) .... ***Melanomyza*** Malloch 11

Face flat, dull (Fig. 4) 12

11. Antennal scape longer than wide, usually with apical hairs below. First flagellomere about four times longer than wide (Fig. 16). Face very swollen, with V-shaped depression below .... ***Melanomyza*** (***Lauxaniella*** Malloch)

3 spp.; southeastern and southern

Scape not longer than wide, bare below. First flagellomere less than three times longer than wide. Face moderately swollen, without well-defined V-shaped depression below (Figs. 2, 41) .... ***Melanomyza*** (***Melanomyza*** Malloch)

5 spp.; widespread

12. Ocellar setae long, parallel, reaching beyond base of antennae in dorsal view .... ***Deceia*** Malloch

2 spp.; central and southern U.S.A.

Ocellar setae short, divergent (Fig. 19) 13

13. Arista long plumose (Fig. 4). Head and body dark brown above, pale below .... ***Trivialia*** Malloch

1 sp., *fuscocapitata* (Malloch); southeastern U.S.A.

Arista pubescent. Head and body yellow, often with black spots or vittae .... ***Poecilominettia*** Hendel, in part

6 spp.; widespread

14. Basal part of Rs with one or two fine hairs above (Fig. 23). Thorax polished black. Head as in Fig. 5 .... ***Xenochaetina*** Malloch

1 sp., *muscaria* (Loew); southeastern U.S.A.

Basal part of Rs bare. Thorax gray pruinose with dark vittae. Head not as above 15

15. First flagellomere less than three times longer than wide (Fig. 3). Knob of halter white. Wing not as below .... ***Neodeceia*** Malloch

1 sp., *cineracea* (Coquillett); Florida

First flagellomere four or more times longer than wide (Fig. 44). Knob of halter black. Wing sometimes broad (Fig. 22) .... ***Steganolauxania*** Frey

4 spp.; southeastern and southern U.S.A.

16. Face convex, glossy 17

Face flat, dull 19

17. Arista plumose. Ocellar setae hair-like, much weaker than postocellar setae (Fig. 6). Yellow species .... ***Physoclypeus*** Hendel

1 sp., *coquilletti* (Hendel); southeastern U.S.A.

Arista pubescent or bare. Ocellar setae equal to or longer than postcellar setae (Fig. 13) 18

18. Arista thickly white pubescent. First flagellomere about five times longer than wide (Fig. 13) .... ***Lauxania*** Latreille

2 spp.; widespread

Arista bare or almost so. First flagellomere usually less than four times longer than wide (Figs. 8, 9) .... ***Pseudocalliope*** Malloch

4 spp.; widespread

19. Postsutural intra-alar seta absent (as in Figs. 47–49) 20

Postsutural intra-alar seta present (Fig. 31) 27

20. Three dorsocentral setae present 21

Four dorsocentral setae present 25

21. Wing with supplementary crossvein joining R_{4+5} and M_1 beyond crossvein dm-cu (Fig. 26). Frons concave in profile (Fig 10) .... ***Xeniconeura*** Shewell

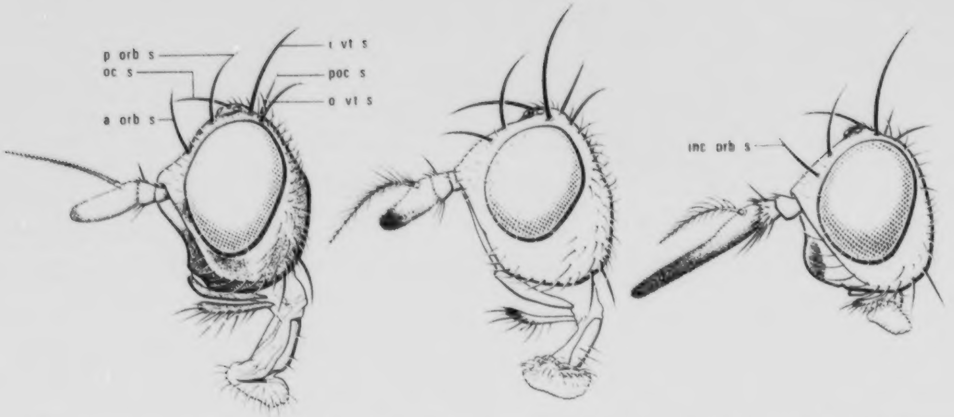
1 sp., *costalis* (Curran); southwestern

Wing without a crossvein beyond dm-cu. Frons not concave in profile 22

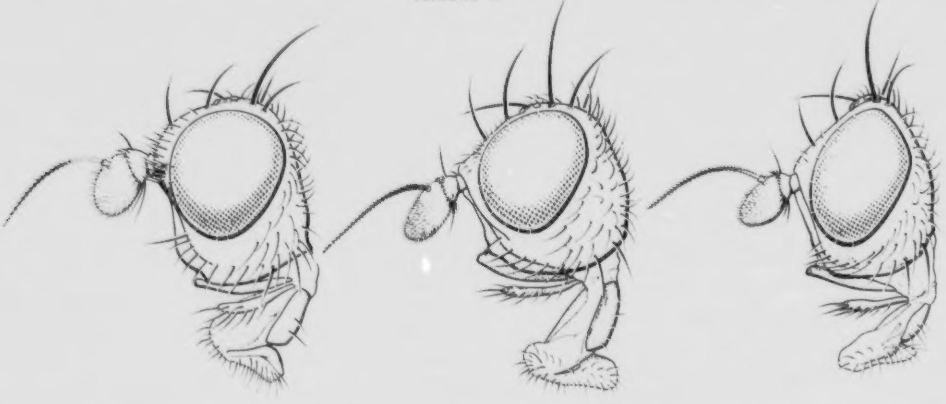
22. Presutural supra-alar seta absent. Head sharply pointed; face strongly retreating (Fig. 7) .... ***Trigonometopus*** Macquart

2 spp.; central and southern

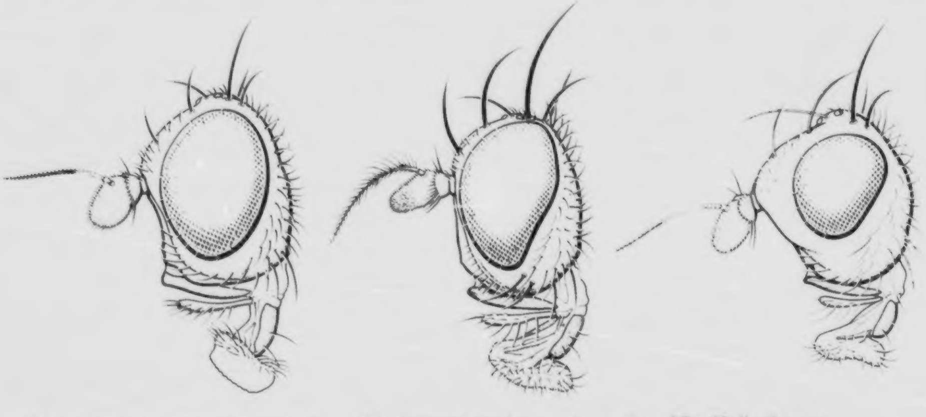
Presutural supra-alar present (Fig. 31). Head not sharply pointed 23



32 Calliopum quadrisetosum ♀ **33** Camptoprosopella borealis ♂ **34** Pachyopella sp. ♀



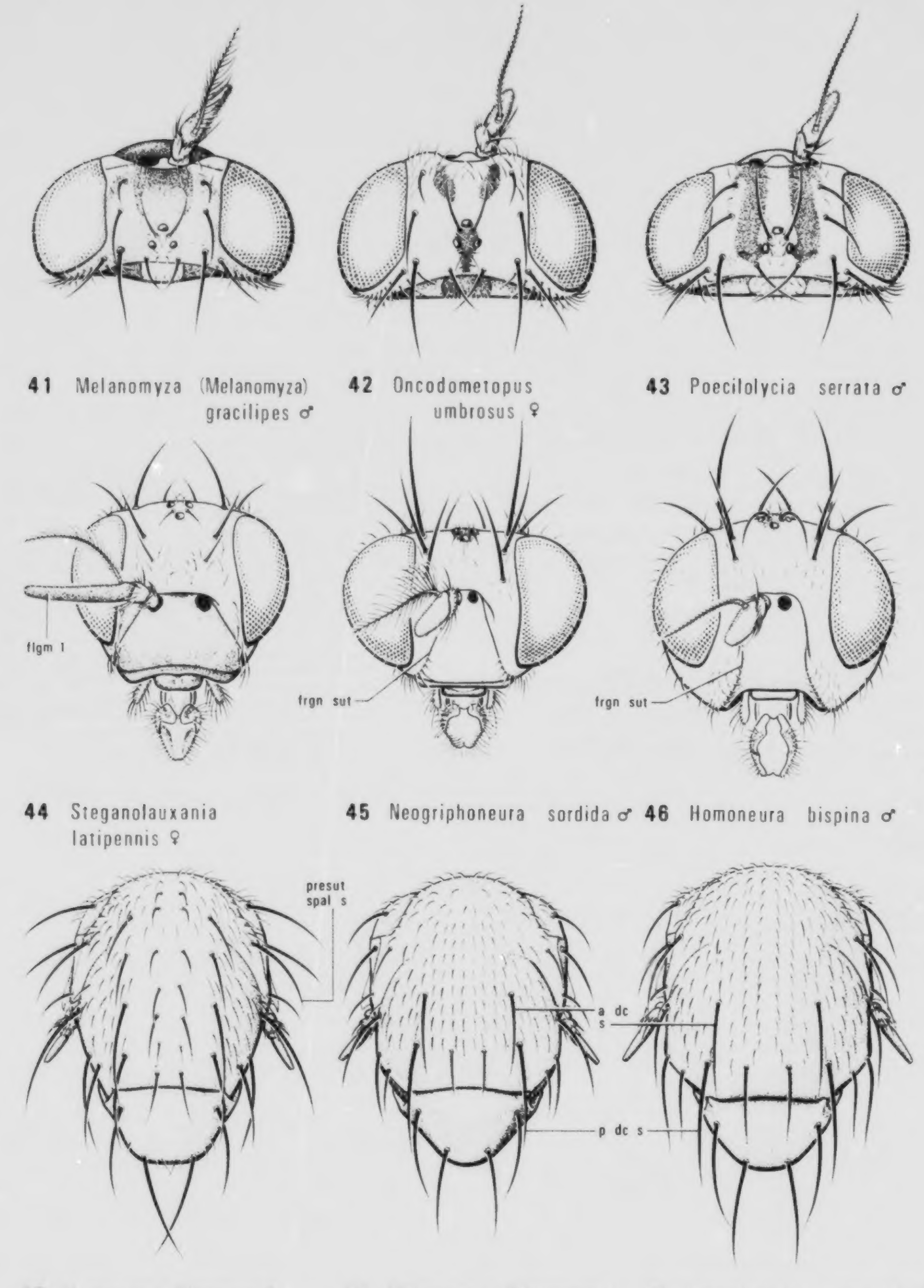
35 Oncodometopus umbrosus ♂ **36** Lyciella discolor ♂ **37** Poecilolycia serrata ♂



38 Sapromyza rotundicornis ♂ **39** Deutominettia geniseta ♀ **40** Mallochomyza citreifrons ♂

Figs. 87.32–40. Lateral views of heads (*continued*): (32) *Calliopum quadrisetosum* (Thomson); (33) *Camptoprosopella borealis* Shewell; (34) *Pachyopella* sp.; (35) *Oncodometopus umbrosus* (Loew); (36) *Lyciella discolor* (Cresson); (37) *Poecilolycia serrata* (Malloch); (38) *Sapromyza rotundicornis* Loew; (39) *Deutominettia geniseta* (Malloch); (40) *Mallochomyza citreifrons* (Malloch).

Abbreviations: a orb s, anterior orbital seta; inc orb s, inclinate orbital seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; poc s, postocellar seta; p orb s, posterior orbital seta.



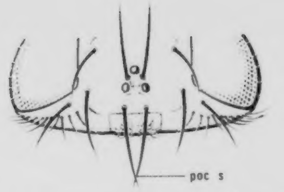
41 Melanomyza (Melanomyza) gracilipes ♂ 42 Oncodometopus umbrosus ♀ 43 Poecilolycia serrata ♂

44 Steganolauxania latipennis ♀ 45 Neogriphoneura sordida ♂ 46 Homoneura bispina ♂

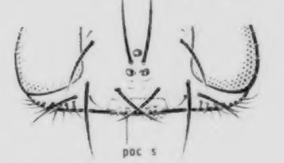
47 Homoneura (Homoneura) philadelphica ♂ 48 Melanomyza (Melanomyza) gracilipes ♂ 49 Xenochaetina muscaria ♀

Figs. 87.41–49. Heads (*continued*) and thoraces (*concluded*): dorsal views of heads of (41) *Melanomyza* (*Melanomyza*) *gracilipes* (Loew), (42) *Oncodometopus umbrosus* (Loew), and (43) *Poecilolycia serrata* (Malloch); frontal views of heads of (44) *Steganolauxania latipennis* (Coquillett), (45) *Neogriphoneura sordida* (Wiedemann), and (46) *Homoneura bispina* (Loew); thoracic dorsum of (47) *Homoneura* (*Homoneura*) *philadelphica* (Macquart), (48) *Melanomyza* (*Melanomyza*) *gracilipes*, and (49) *Xenochaetina muscaria* (Loew).

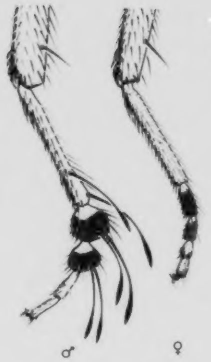
Abbreviations: a dc s, anterior dorsocentral seta; flgm, flagellomere; frgn sut, frontogenal suture; p dc s, posterior dorsocentral seta; presut spal s, presutural supra-alar seta.



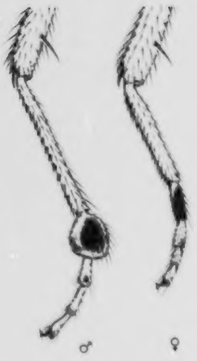
50 Homoneura (Tarsohomoneura) americana ♂



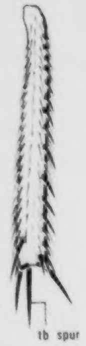
51 Homoneura (Homoneura) philadelphica ♂



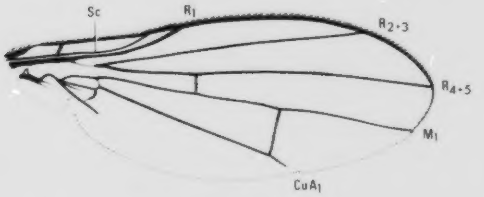
52 Homoneura (Tarsohomoneura) ornatipes



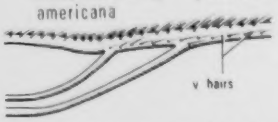
53 Homoneura (Tarsohomoneura) americana



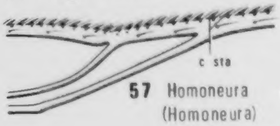
54 Deutominettia geniseta ♀



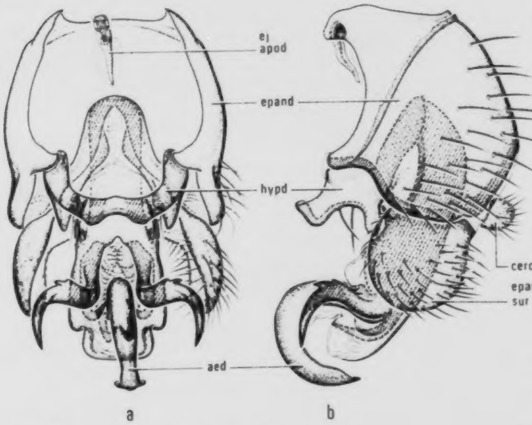
55 Mallochomyza citreifrons ♂



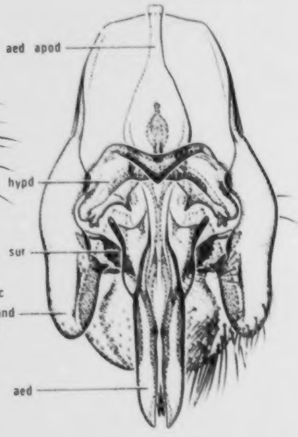
56 Neogriphoneura sordida ♂



57 Homoneura (Homoneura) philadelphica ♂



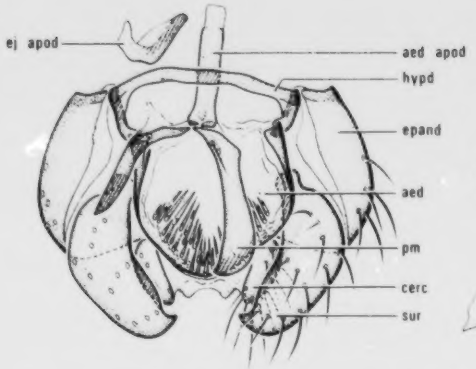
58 Calliopum quadrisetosum ♂



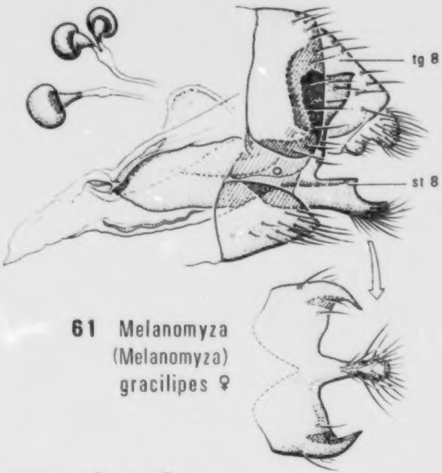
59 Homoneura (Tarsohomoneura) ornatipes ♂

Figs. 87.50–59. Heads, legs, and wings (*concluded*), and male terminalia: dorsal views of vertex of (50) ***Homoneura (Tarsohomoneura) americana*** (Wiedemann) and (51) ***Homoneura (Homoneura) philadelphica*** (Macquart); anterior views of left hind tarsus of male and female of (52) ***Homoneura (Tarsohomoneura) ornatipes*** (Johnson) and (53) ***Homoneura (Tarsohomoneura) americana***; (54) dorsal view of right middle tibia of ***Deutominettia geniseta*** (Malloch); (55) wing of ***Mallochomyza citreifrons*** (Malloch); details of ventral side of pterostigmal area of left wing of (56) ***Neogriphoneura sordida*** (Wiedemann) and (57) ***Homoneura (Homoneura) philadelphica***; (58*a*) ventral and (58*b*) lateral views of male terminalia of ***Calliopum quadrisetosum*** (Thomson); (59) ventral view of male terminalia of ***Homoneura (Tarsohomoneura) ornatipes***.

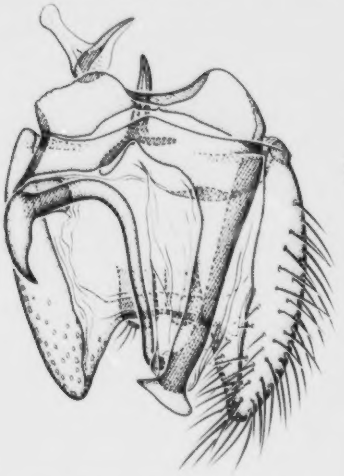
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; c sta, costal setulae; ej apod, ejaculatory apodeme; epand, epandrium; hypd, hypandrium; poc s, postocellar seta; sur, surstylus; tb spur, tibial spur; v hairs, ventral hairs.



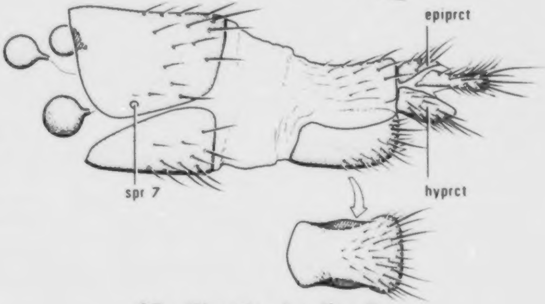
60 Minettia lupulina ♂



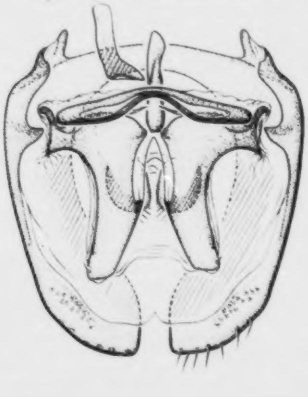
61 Melanomyza (Melanomyza) gracilipes ♀



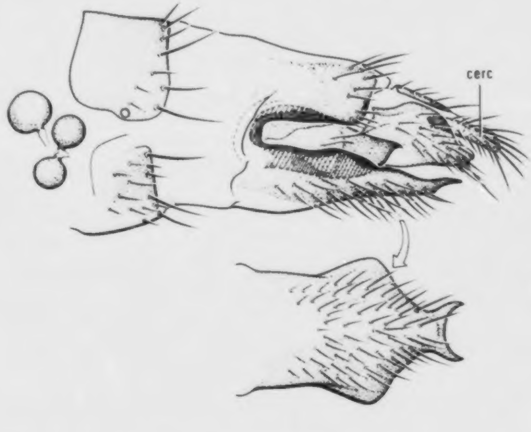
62 Sapromyza rotundicornis ♂



63 Minettia lupulina ♀



64 Trigonometopus vittatus ♂



65 Sapromyza nigrans ♀

Figs. 87.60–65. Male and female terminalia (*concluded*): ventral views of male terminalia of (60) ***Minettia lupulina*** (Fabricius), (62) ***Sapromyza rotundicornis*** Loew, and (64) ***Trigonometopus vittatus*** Loew; lateral views of female terminalia, with outline of sternite 8 in ventral view, of (61) ***Melanomyza*** (***Melanomyza***) ***gracilipes*** (Loew), (63) ***Minettia lupulina***, and (65) ***Sapromyza nigrans*** (Melander).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spr, spiracle; st, sternite; sur, surstylus; tg, tergite.

23. Dorsocentral setae arranged 1 + 2. Head as in Figs. 12 and 15 .... ***Trisapromyza*** Shewell

1 sp., *vittigera* (Coquillett); eastern

Dorsocentral setae arranged 0 + 3 24

24. Frons with distinct orbito-antennal spot present; anterior margin of frons including spot conspicuously haired (Fig. 42). Uppermost hair of parafacial row long (Fig. 35). Presutural supra-alar seta reduced, equal to or shorter than posterior notopleural seta .... ***Oncodometopus*** Shewell

1 sp., *umbrosus* (Loew); eastern and southern U.S.A.

Frons without an orbito-antennal spot, without hairs lateral to base of antenna. Parafacial row uniform (Fig. 38). Presutural supra-alar seta longer than posterior notopleural seta .... ***Sapromyza*** Fallén[1]

9 spp.; widespread

25. Pale yellow species. Frons swollen (Fig. 40). Ventral hairs and setae mostly pale. Wing with at least faint isolated spots (Fig. 55). .... ***Mallochomyza*** Hendel

1 sp., *citreifrons* (Malloch); widespread

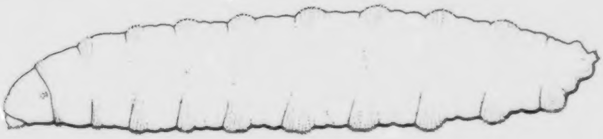
Species not yellow 26

26. Four pairs of acrostichal setae present. Hind femur with a strong anteroventral seta beyond middle. Wing irrorated (Fig. 25) .... ***Trypetisoma*** Malloch

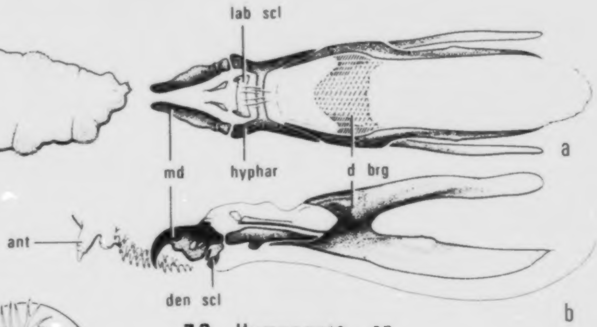
2 spp.; southern; Arnaud 1968

Only prescutellar pair of acrostichal setae present. Hind femur without anteroventral seta. Wing unmarked. Head as in Figs. 37 and 43 .... ***Poecilolycia*** Shewell

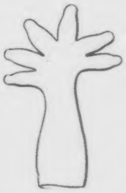
11 spp.; widespread; Shewell 1938 (*Sapromyza*, in part)



66 Homoneura sp.



70 Homoneura sp.



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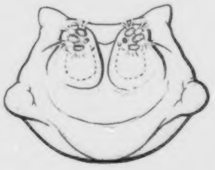

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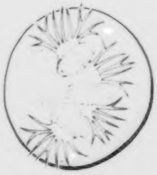

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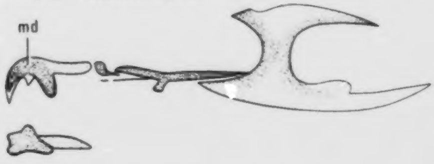
Homoneura sp.



71 Homoneura (Tarsohomoneura) americana

Figs. 87.66–71. Immature stages of *Homoneura* spp.: (66) lateral view of third instar larva; (67) anterior spiracle; (68) posterior spiracular disc; (69) posterior spiracular plate; (70*a*) ventral and (70*b*) lateral views of cephalopharyngeal skeleton; (71) lateral view of cephalopharyngeal skeleton and dorsal view of mandible of first instar larva of *Homoneura* (*Tarsohomoneura*) *americana* (Wiedemann). Drawings of first instar after Miller and Foote (1976).

Abbreviations: ant, antenna; d brg, dorsal bridge; den scl, dental sclerite; hyphar, hypopharynx; lab scl, labial sclerite; md, mandible.

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[1] Includes the two subgenera *Sapromyza s. str.* and *Schumannimyia* Papp (Papp 1978).

27. Wing with supplementary crossvein joining R_{4+5} and M_1 beyond crossvein dm-cu (Fig. 24) .... ***Xenopterella*** Malloch

1 sp., *beameri* Steyskal; southwestern

Wing without a crossvein beyond crossvein dm-cu 28

28. Middle tibia with three apical spurs (Fig. 54). A strong seta present on gena near lower margin of eye (Fig. 39) .... ***Deutominettia*** Hendel

1 sp., *geniseta* (Malloch); southwestern

Middle tibia with one apical spur (Fig. 28). No strong genal seta present near lower margin of eye (Figs. 32–38) 29

29. Ocellar setae divergent, weaker than postocellar setae (Fig. 19) .... ***Poeciliominettia*** Hendel, in part

see couplet 13

Ocellar setae parallel, stronger than postocellar setae (Fig. 18) .... ***Minettia*** Robineau-Desvoidy 30

30. Prosternum bare. Black species .... ***Minettia*** (***Frendelia*** Collin)

5 spp.; widespread; Steyskal 1971

Prosternum haired. Species not black .... ***Minettia*** (***Minettia*** Robineau-Desvoidy)

11 spp.; widespread; Malloch and McAtee 1924

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CHAMAEMYIIDAE

88

J. F. McAlpine

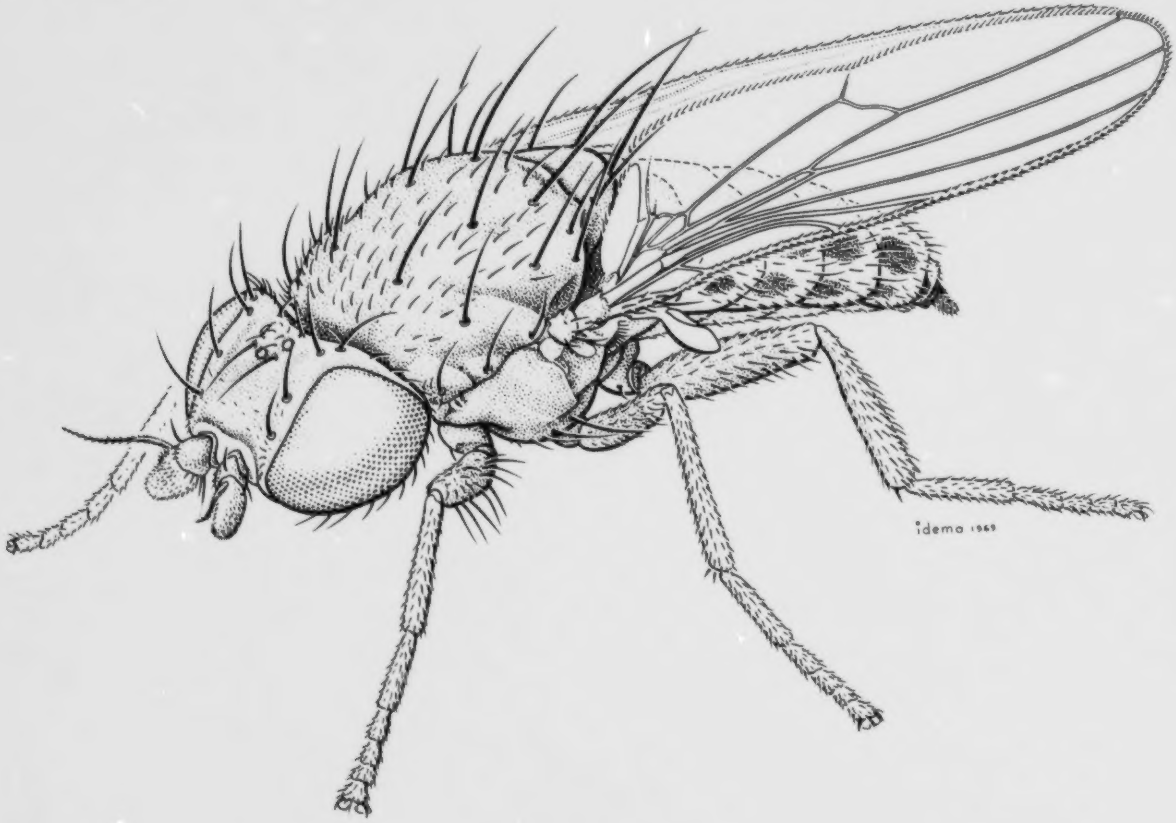


Fig. 88.1. Female of *Chamaemyia polystigma* (Meigen).

Small stocky flies (Fig. 1) about equal in size to drosophilids, 1.0–4.0 mm long, silvery gray to brown, usually densely pruinose, occasionally shining black, often with brown stripes on thorax and black spots or bands on abdomen. Wing usually uniformly milky hyaline, occasionally with brown markings.

Adult. Head: as broad as or broader than thorax, longer than high and pointed anteriorly (Fig. 2) to higher than long and rounded anteriorly (Figs. 3–8). Compound eye elongate oval (Fig. 1) to nearly round (Fig. 6), bare to shortly pubescent. Frons broad to narrow, slightly narrower in male than in female in some groups, e.g. *Neoleucopis* Malloch (Fig. 6); sides more or less parallel; entire frons with numerous fine setulae as well as bristles; zero (Fig. 8) to three (Fig. 2) fronto-orbital bristles present. Ocellar triangle occasionally enlarged and prominent (Fig. 8); ocellar bristles strong to absent, when present usually proclinate (Figs. 2–5), sometimes reclinate (Figs. 6, 7); inner and outer vertical bristles usually present, sometimes reduced or absent; postocellar bristles convergent (Figs. 2–4), sometimes minute or absent, e.g. in *Leucopis* Meigen (Figs. 5–8). Lunule small, narrowly exposed, and bare (Figs. 2–5) to large, broadly exposed, and setulose (Figs. 6–8). Face gently concave (Figs. 3–8) to strongly receding (Fig. 2), without deep antennal grooves. Vibrissae absent; gena with a row of subvibrissal hairs, including a genal bristle (Figs. 2–8). Antenna short and porrect; first flagellomere usually oval (Figs. 3–8), rarely twice as long as wide (Fig. 2); pedicel about as long as broad, without a dorsal seam, and with or without a conspicuous dorsal bristle; arista bare or very shortly pubescent, never plumose. Proboscis short; palpus small.

Thorax: scutum (Figs. 12, 13) with numerous neatly arranged setulae and bristles, never hairy, frequently with brown dorsocentral stripes; one postpronotal, one presutural supra-alar, two notopleural, one postsutural supra-alar, and two postalar bristles present; zero to two presutural and two to four postsutural dorsocentral bristles present; prescutellar acrostichal bristles present or absent, weak or strong; acrostichal setulae in zero to ten rows. Prescutellum usually developed (Figs. 1, 13); scutellum with four bristles, never with additional hairs or setulae. Anepisternum with or without setulae and bristles; anepimeron bare except in some *Cremifania* species; katepisternum with one strong bristle and additional setulae. Proepisternal bristle absent, except in Australian genus *Pseudoleucopis* Malloch; proepimeral bristle absent; remaining pleural sclerites bare. Prosternum free from propleuron, bare. Wing (Figs. 9–11) moderately broad, with well-developed anal lobe and alula; C unbroken, extending to M except in *Lipoleucopis* Meijere (Fig. 11) where it ends at R_{4+5}; Sc complete and free; R suddenly approaching Sc closely near apex of Sc; cells bm and dm usually separated by crossvein bm-cu except in Neotropical genus *Melaleucopis* Sabrosky and in some *Leucopis* spp.; cell cu*p* present; A_1 abruptly discontinued at basal third to half. Legs rather weakly bristled; bristles strongest on fore femur; all tibiae without a preapical dorsal bristle.

Abdomen: abdominal tergites 1–5 (Fig. 14) frequently with blackish fasciae or paired spots (Fig. 1). Seven pairs of spiracles present in membrane in both sexes (Figs. 15, 16).

One or two separate sclerites present dorsally in male between tergite 5 and epandrium, i.e. tergite 6 frequently absent or fused with syntergosternite 7 + 8 (Fig. 15); similarly one or two separate sclerites present ventrally between sternite 5 and hypandrium, i.e. sternite 6 frequently absent or fused with sternite 7 (Fig. 15). Male terminalia symmetric. Surstylus usually absent or fused with lower lateral margin of epandrium to form an unarticulated surstylar lobe (Fig. 15), but present and free in *Cremifania* Czerny. Aedeagus usually a simple heavily sclerotized, elongate tube that is more or less C-shaped (Fig. 15) but which is long and flexible in *Cremifania*; aedeagal apodeme usually fused to hypandrium, but free and rod-like in *Cremifania*; gonopod and paramere heavily sclerotized processes, more or less fused at their bases. Cerci fairly large, frequently heavily sclerotized at apices.

Female with abdominal sternites and tergites 1–7 well-developed (Figs. 16, 17); tergite 7 and sternite 7 free; sternite 6 frequently larger, broader, and more heavily sclerotized than sternite 5; sternite 7 sometimes divided along midline. Terminalia weakly sclerotized, flexible, and telescopically tube-like. Tergite 8 and sternite 8 clearly present to absent. Epiproct and hypoproct discrete. Cerci fairly large, oval, and weakly sclerotized. Four sclerotized spermathecae present, except in *Cremifania* which has three.

Larva. Rather stout, triangular in outline, grub-like as in some Syrphidae, somewhat dorsoventrally compressed, with conspicuous intersegmental annuli (Fig. 21). Cuticle rough and wrinkly, usually bearing numerous spinules, papillae, and tubercles as in Sciomyzidae, whitish through yellow brown to greenish, frequently covered with a grayish waxy substance. Cephalopharyngeal sclerites simple (Fig. 18); dental sclerite present and toothed in *Cremifania*, otherwise absent; hypopharyngeal and tentoropharyngeal sclerites fused; parastomal bar usually, perhaps always, absent. Anterior spiracle with 4–12 digits arranged fanwise. Posterior spiracles (Figs. 19, 20) on more or less elongate heavily sclerotized spiracular processes; each spiracle with three radially arranged slits. Interstigmatal processes few to numerous, and usually, if not always, unbranched.

Biology and behavior. Larvae of most species are free-living predators of adelgids, aphids, coccids, and scales (Barber 1985; Sluss and Foote 1971, 1973; McAlpine and Tanasijtschuk 1972; Tanasijtschuk 1970). Because they are effective as biological control agents against these insects, some species have been purposely introduced in Canada and the United States to control economically important pests; for example *Cremifania nigrocellulata* Czerny (Delucchi and Pschorn-Walcher 1954), *Leucopis (Neoleucopis) atratula* Ratzeburg (McAlpine 1971), and *Leucopis (Leucopis) hennigrata* McAlpine (McAlpine 1978) were introduced to control *Adelges piceae* (Ratzeburg).

Classification and distribution. The family as defined by McAlpine (1960, 1963) has two subfamilies, Cremifaniinae and Chamaemyiinae, containing about 20 world genera and subgenera, two-thirds of which occur in North America. The taxonomy of the species in many groups is poorly known, and revisions of most genera are required. An estimated 100–150 species occur in the Nearctic region, about half of which are undescribed. One fossil species is known, *Procremifania electrica* Hennig from Baltic amber (Hennig 1965).

The genus *Paraleucopis* is here included in the key to the genera of the Chamaemyiidae as a matter of convenience. Although its placement in this family has always been accepted, it really belongs elsewhere. The male and female terminalia differ radically from those of Chamaemyiidae, and the habits of the larvae (inhabitants of bird's nests) are also very different. *Paraleucopis* is closely related to *Gayomyia* Malloch (Chile, Australia) and *Schizostomyia* Malloch (Chile), and all three genera are allied to Asteiidae (see J. F. McAlpine, Ch. 116, under Asteiidae).

Key to genera

1. Pterostigmal space subequal in length to cell c and unusually darkly clouded (Fig. 4.61). Prescutellum and presutural supra-alar bristle absent. Male with movable bilobate surstylus; aedeagus flexible and with spine-like subapical armature; aedeagal apodeme free, cuneiform. Female with three spermathecae . . . . CREMIFANIINAE . . . . ***Cremifania*** Czerny
2 spp.; McAlpine 1963

Pterostigmal space seldom half as long as cell c, usually lightly clouded (Figs. 9–11). Prescutellum usually present (Fig. 13), but absent in *Lipoleucopis*, *Paraleucopis* (Fig. 12), and some *Leucopis*; presutural supra-alar bristle present (Fig. 13) (absent in *Paraleucopis* (Fig. 12)). Male without a movable surstylus (movable in *Paraleucopis*); aedeagus rigid and without spine-like armature (Fig. 15); aedeagal apodeme fused with hypandrium. Female with four spermathecae (Figs. 16, 17) (with two or three in *Paraleucopis*) .... CHAMAEMYIINAE....2

2. Lunule bare, usually narrow from anterior to posterior border and more or less concealed; orbital plate with one or more strong bristles (Figs. 2–4) (weak in *Paraleucopis* Malloch, Fig. 5); postocellar bristles present (Figs. 2–4) (absent in some *Paraleucopis*, Fig. 5); apical section of $A_1 + CuA_2$ extending far beyond apex of cell cu*p* (Fig. 9) .... CHAMAEMYIINI....3

Lunule finely setulose, usually wide and exposed; orbital bristles weak or absent; postocellar bristles absent (Figs. 6–8); apical section of $A_1 + CuA_2$ ending close to apex of cell cu*p* (Fig. 11) .... LEUCOPINI....8

3. Postocellar, presutural intra-alar, and postsutural supra-alar bristles absent (Figs. 5, 12); some fine setulae on scutum. Shining black species with little or no pruinescence .... ***Paraleucopis*** Malloch

2 spp.; southwestern U.S.A.; Steyskal 1971, 1981

Postocellar, presutural intra-alar, and postsutural supra-alar bristles present (Figs. 2–4, 13); setulae present or absent on scutum. Usually densely pruinose species, seldom shining black 4

4. Proepisternal bristle present .... ***Pseudoleucopis*** Malloch

1 sp., *benefica* Malloch; Australia, introduced in California, doubtfully established in North America; larvae predators of scale insects

Proepisternal bristle absent 5

5. Anepisternum with one bristle; presutural dorsocentral bristles absent (as in Figs. 12, 13) .... ***Pseudodinia*** Coquillett

17 spp.; widespread; Malloch 1940, Barber 1985

Anepisternum bare; presutural dorsocentral bristles present (Fig. 1) 6

6. Scutum with one presutural and two postsutural dorsocentral bristles (Fig. 1) .... ***Chamaemyia*** Meigen

6–10 spp.; widespread; larvae predators of scale insects on roots and leaf sheaths of grasses

Scutum with one presutural and three postsutural dorsocentral bristles 7

7. Wing with reticulate pattern (Fig. 9). Head extremely pointed in side view, with lowermost fronto-orbital bristle about midway between lunule and upper orbital bristle (Fig. 2) .... ***Toropamecia*** Cogan

2 spp.; southeastern U.S.A.; Steyskal 1972, Cogan 1978

Wing uniformly milky hyaline (Figs. 10, 11). Head less pointed in side view, with lowermost fronto-orbital bristle closer to lunule than to upper orbital bristle (Fig. 3) .... ***Plunomia*** Curran

4 spp.; widespread; Malloch 1940

8. C ending at R_{4+5} (Fig. 11). Prescutellum absent (as in Fig. 12) ..... ***Lipoleucopis*** Meijere

1 sp., *praecox* Meijere; Holland, introduced in New Brunswick, doubtfully established in North America

C reaching M (as in Figs. 9, 10). Prescutellum usually present (Fig. 13) .... ***Leucopis*** Meigen....9

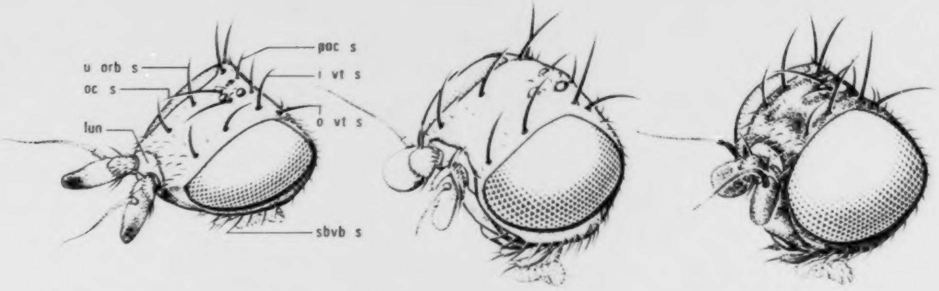
9. Prescutellar acrostichal bristles present (Fig. 13) 10

Prescutellar acrostichal bristles absent (as in Fig. 12) 12

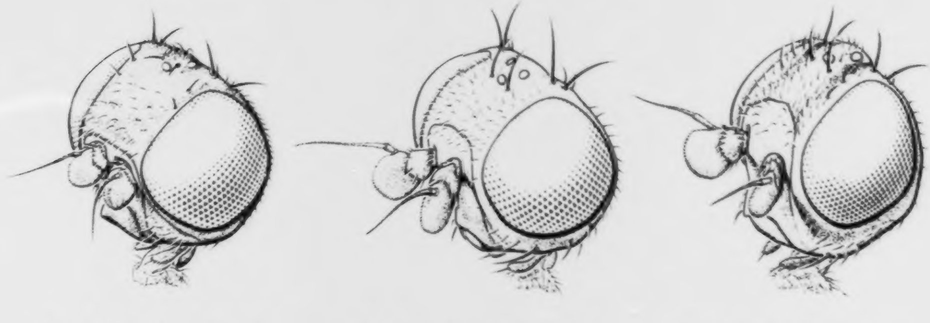
10. Ocellar bristles present, reclinate (Fig. 6). Scutum without dorsocentral stripes .... ***Leucopis*** (***Neoleucopis*** Malloch)

4–6 spp., some introduced; widespread; larvae predators of Adelgidae; McAlpine 1971

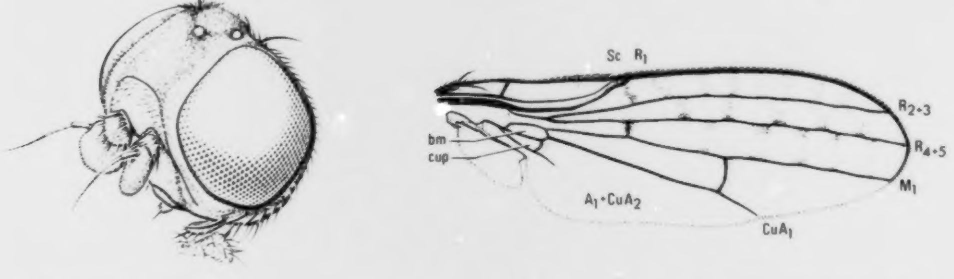
Ocellar bristles absent. Scutum with or without dorsocentral stripes 11



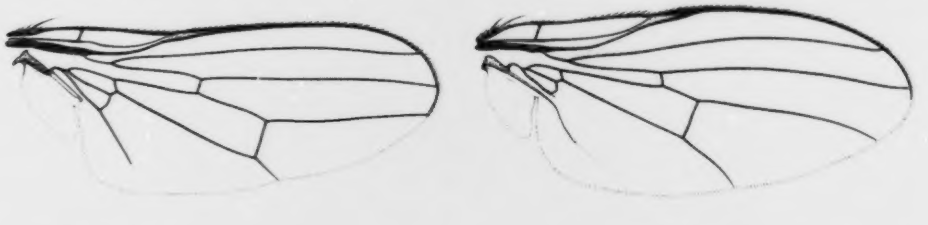
2 Toropamecia punctata ♂ **3** Plunomia elegans ♀ **4** Pseudodinia varipes ♂



5 Paraleucopis corvina ♀ **6** Leucopis (Neoleucopis) pinicola ♀ **7** Leucopis (Xenoleucopis) sp. ♂



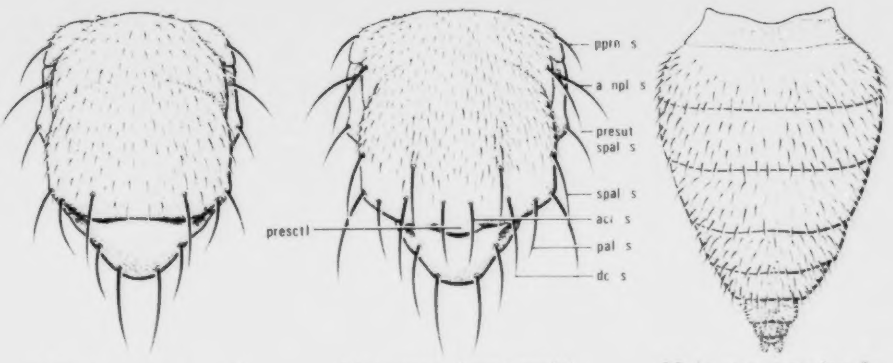
8 Leucopis ocellaris ♂ **9** Toropamecia punctata ♂



10 Paraleucopis corvina ♀ **11** Lipoleucopis praecox ♂

Figs. 88.2–11. Heads and wings: heads of (2) *Toropamecia punctata* (Coquillett), (3) *Plunomia elegans* Curran, (4) *Pseudodinia varipes* Coquillet, (5) *Paraleucopis corvina* Malloch, (6) *Leucopis (Neoleucopis) pinicola* Malloch, (7) *Leucopis (Xenoleucopis)* sp., and (8) *Leucopis ocellaris* Malloch; wings of (9) *Toropamecia punctata*, (10) *Paraleucopis corvina*, and (11) *Lipoleucopis praecox* Meijere.

Abbreviations: i vt s, inner vertical seta; lun, lunule; oc s, ocellar seta; o vt s, outer vertical seta; poc s, postocellar seta; sbvb s, subvibrissal seta; u orb s, upper orbital seta.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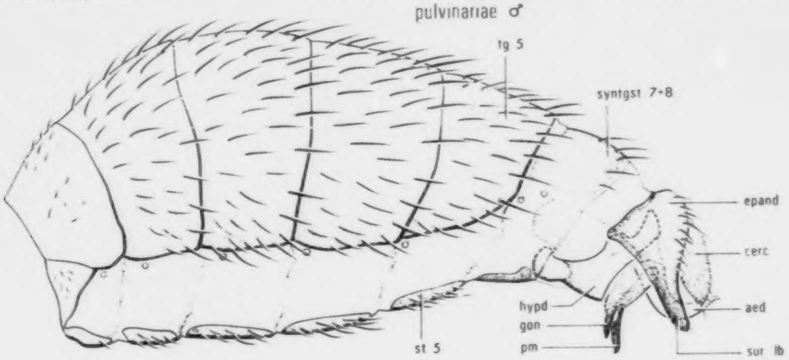
12 Paraleucopis corvina ♀ 13 Leucopis (Leucopomyia) pulvinariae ♂ 14 Leucopis geniculata ♀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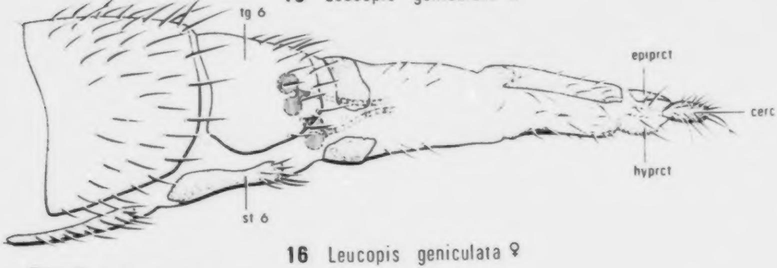
15 Leucopis geniculata ♂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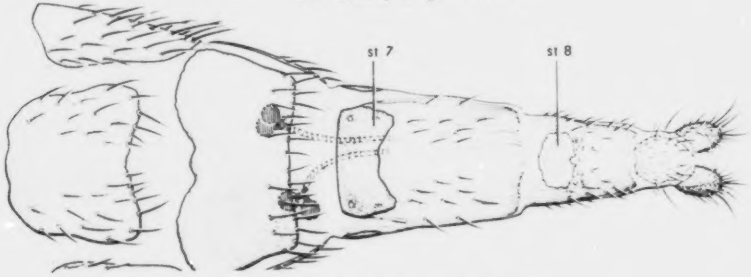
16 Leucopis geniculata ♀



17 Leucopis geniculata ♀

Figs. 88.12–17. Thoraces and abdomens: thoraces of (12) *Paraleucopis corvina* Malloch and (13) *Leucopis (Leucopomyia) pulvinariae* Malloch in dorsal view; male abdomen of *Leucopis geniculata* Zetterstedt in (14) dorsal view and (15) left lateral view; female terminalia of *Leucopis geniculata* in (16) left lateral view and (17) ventral view. Abbreviations: acr s, acrostichal seta; aed, aedeagus; a npl s, anterior notopleural seta; cerc, cercus; dc s, dorsocentral seta; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pal s, postalar seta; pm, paramere; pprn s, postpronotal seta; presctl, prescutellum; presut spal s, presutural supra-alar seta; spal s, supra-alar seta; st, sternite; sur lb, surstylar lobe; syntgst, syntergosternite; tg, tergite.

11. Scutum with brown dorsocentral stripes (as in Fig. 13); prescutellum present .... ***Leucopis*** **(*Leucopomyia*** Malloch)

1 sp., *pulvinariae* Malloch; widespread; larvae predators of mealy bugs on grasses

Scutum unicolorous gray, without brown dorsocentral stripes; prescutellum absent .... ***Leucopis*** **(*geniculata*** group)

1 sp., *geniculata* Zetterstedt; Holarctic; larva predator of adelgids

12. Ocellar plate expanded and densely pilose or setulose; posterior ocelli much farther from each other than from anterior ocellus; weak ocellar or orbital setulae, or both, frequently evident in female (Fig. 8) .... ***Leucopis*** **(*ocellaris*** group)

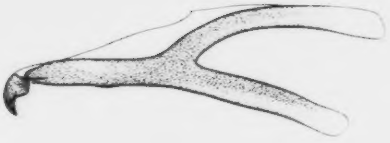
5 descr., many undescr. spp.; widespread; larvae predators of scale insects

Ocellar plate not expanded, but sometimes at least partially enclosed by adjacent velvety pads; ocelli forming a nearly equilateral triangle; ocellar or orbital setulae, or both, sometimes present in both sexes (Fig. 7) 13

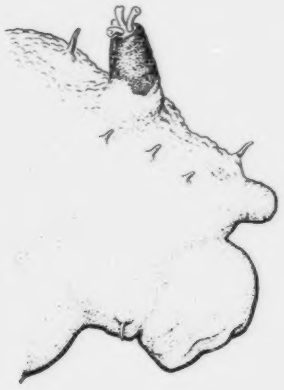
13. Frons with one to several distinguishable orbital or ocellar bristles, or both (Fig. 7) .... ***Leucopis*** **(*Xenoleucopis*** Malloch)

Frons without discrete orbital or ocellar bristles .... ***Leucopis*** **(*Leucopis*** Meigen)

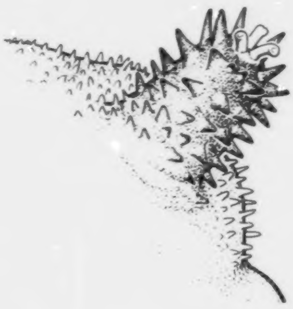
many species; widespread; larvae predators of adelgids and aphids



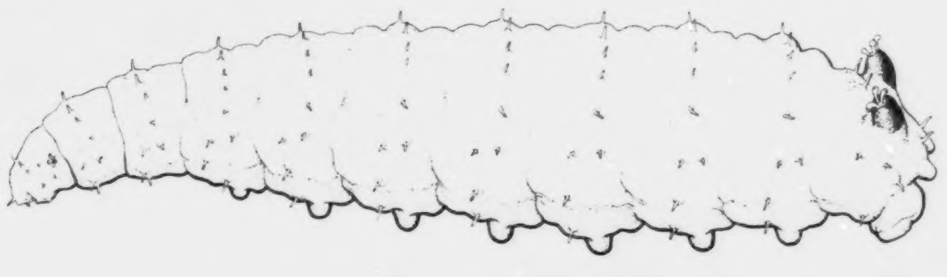
18 Leucopis (Leucopis) simplex



19 Leucopis (Leucopis) simplex



20 Leucopis (Leucopis) sp.



21 Leucopis (Leucopis) simplex

Figs. 88.18–21. Larval features: (18) cephalopharyngeal skeleton, (19) details of terminal abdominal segment, and (21) entire larva of *Leucopis (Leucopis) simplex* Loew, left lateral view; (20) details of posterior spiracle of *Leucopis (Leucopis)* species near *atrifacies* Aldrich.

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HELEOMYZIDAE

89

GORDON D. GILL AND B. V. PETERSON

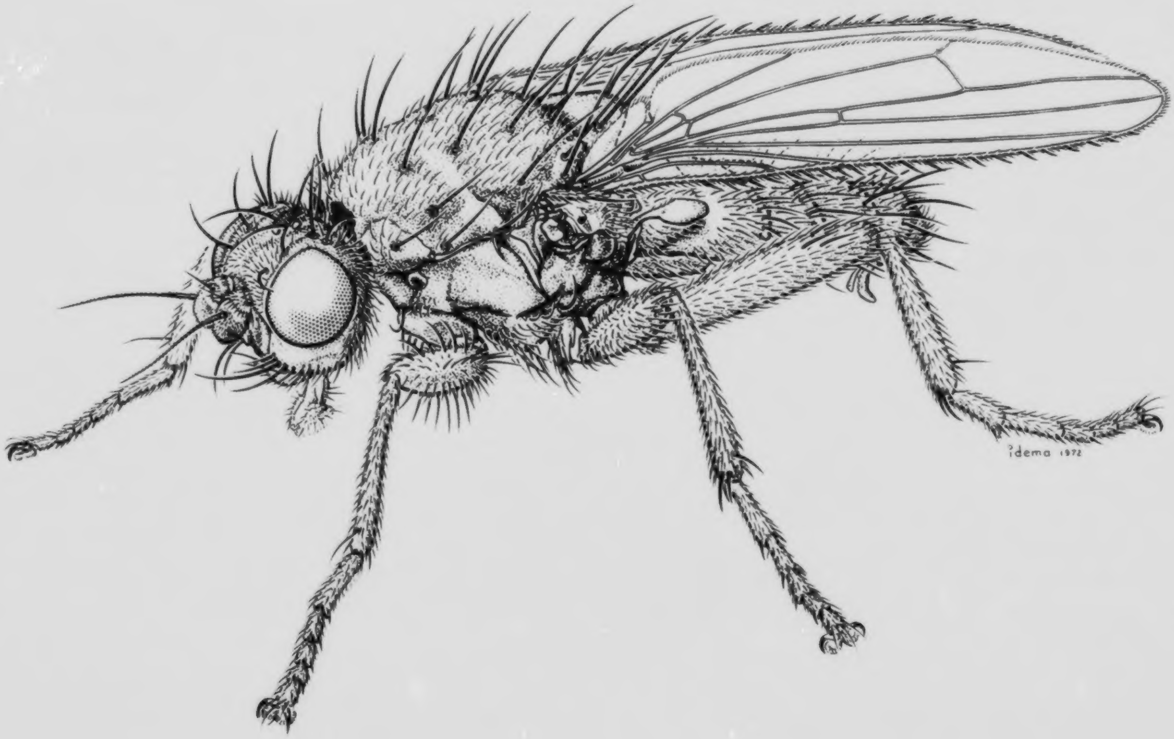


Fig. 89.1. Male of *Heleomyza serrata* (Linnaeus).

Moderately bristly flies (Fig. 1) varying from 2.0–11.0 mm in length but usually 3.0–7.0 mm long, often distinctly pruinose, and yellow, reddish yellow, or reddish brown to black in color. Antenna short; orbital plate of frons usually differentiated; face vertical or receding. Wing usually with costal spines and crossveins often clouded; mid and hind tibiae usually with preapical dorsal bristles.

Adult. Head: eyes widely separated at vertex (except in male of *Heteromyza oculata* Fallén). Frons usually broad, sometimes slightly narrowed anteriorly; orbital plates present as strips, usually pruinose, extending forward from vertical bristles (Figs. 2–5). One, two, or three orbital bristles present in Nearctic species, reclinate or outwardly directed; scattered setae often present on frons; ocellar and inner and outer vertical bristles strong; postocellar bristles convergent; one (rarely two) pair of oral vibrissae present, with one or more rows of subvibrissal setae and one or two strong genal setae. Antenna with first flagellomere rounded in lateral view; arista minutely pubescent to plumose. Proboscis fleshy; palpus well-developed.

Thorax: scutum (Figs. 1, 5) with one prescutellar acrostichal bristle or none; acrostichal setae variable; dorsocentral bristles variable, usually four or five present, with one or more anterior bristles often very much weakened; postpronotal bristle present or absent; two notopleural and three alar bristles present; scutellum with two or three strong lateral bristles, sometimes with setae dorsally or laterally or both, between bristles, otherwise bare. Proepisternal bristle present or absent. Anepisternum bare or with variably sized setae or bristles; katepisternum with one or more bristles posteriorly, usually with additional anterior and ventral setae; anepimeron bare or with hairs or bristles; meron bare.

Wing (Figs. 6–10) usually hyaline, sometimes with a faint yellowish or brownish tinge, rarely mottled with contrasting whitish and dark gray areas; crossveins often clouded, and sometimes with extensive infuscations along longitudinal veins; wing sometimes mutilated (*Lutomyia* Aldrich, Fig. 10). C extending to end of M_{1+2}, but weakened or broken near apex of Sc, usually with conspicuous spines; Sc usually completely separate from R_1 (Figs. 6, 7), ending in C sometimes close to R_1 (Figs. 8, 9). R_1 variable in length but often rather short; pterostigma often present; CuA_2 short, fusing with A_1 and often nearly reaching wing margin as $CuA_2 + A_1$; A_2 weakly developed or absent. Cells bm and dm completely separated; cell br usually relatively long; cell cu*p* present.

Legs only moderately bristly (Fig. 1), varying among genera and species. Mid tibia with one or more apical ventral bristles; mid and hind tibiae usually with preapical dorsal bristles, but these often fine and hair-like, or indistinguishable in *Borboropsis* Czerny and *Oldenbergiella* Czerny. Pulvilli pad-like; empodia bristle-like; claws moderately long and stout.

Abdomen: broad basally, tapering distally in female, more rounded and knob-like in male; sparsely to moderately bristly; seven pairs of spiracles usually present in membrane of lateral margins of tergites in both sexes, but those of segments 6 and 7 sometimes displaced in male (Figs. 11, 12).

Female with tergites and sternites present and distinct; sternite 8 with a small but usually distinct pair of lobes. Epiproct and hypoproct distinct but usually small. Spermathecae varying from two to four, usually three with one of them being somewhat removed from the other two, all tiny, spherical, and heavily sclerotized. Cerci small but free and distinct.

Male (Figs. 11, 12) with tergites and sternites 1–5 symmetric; tergites and sternites 6–8 usually asymmetric; tergites 6 and 7 variable in size but usually reduced, represented by variably developed sclerotized bands or small plates often displaced to right; these tergites in part fused with their respective sternites; sometimes small plate-like remnants of these tergites present, free in membrane; tergite 6 said to be fused with sternite 8 in *Suillia* Robineau-Desvoidy (Griffiths 1972) but in species examined all elements were distinct; syntergosternite 8 usually large, sometimes at least partially fused with tergite and sternite 7; sternite 8 sometimes present as a small plate or short faintly sclerotized narrow strip on left side. Sternal portion of syntergosternites 6 and 7 variably developed; sternite 6 often larger and more ventral but may be closely associated with sternite 7 on left side ventrolaterally; sternite 7, when present, usually smaller and more lateral, often weakly sclerotized, and sometimes strongly twisted with left end fading and ending near left spiracle 7; spiracle 7 located ventrally and often obscured by aedeagus and thus easily overlooked. Epandrium large, somewhat rounded. Cerci well-developed, usually at least partially fused, taking various shapes. Surstylus sometimes consisting of a single lobe of widely different shapes, or sometimes divided into an anterior and posterior lobe that may be very different in size and shape; these lobes variously ornamented with spinules and setae; sternite 10 prominent, often with variously developed rod-like or plate-like processes that are sometimes beset with various combinations of spinules and setae. Hypandrium broadly U-shaped, often with variously sized and shaped remnants of gonopods that sometimes bear one or more setae; paramere sometimes absent, but when present, variably developed, usually represented by a small often dentate lobe on each side of base of aedeagus, and often with one or more setae; aedeagus variable, sometimes long and slender with various sclerotizations, more rarely broad, somewhat flattened distally, and complex, also with various sclerotizations; aedeagus at rest directed anteriorly; aedeagal apodeme usually well-developed, rod-like, and mostly free from hypandrium to extensively fused with hypandrium; ejaculatory apodeme present, but usually rather short; sperm pump small but distinct.

Egg. White, elongate ovoid, about 0.60–0.70 mm long and 0.23–0.25 mm wide. Micropylar end slightly more pointed and lacking hexagonal cuticular reticulation found on rest of cuticle.

Larva. Elongate conical, tapering anteriorly, bluntly convex posteriorly, chalky white to yellowish white in color, 4.0–11.8 mm long.

Cephalic segment bilobate, with each lobe bearing a dorsal two-segmented antenna and a ventral maxillary palpus surrounded by a C-shaped ring, and with a small papilla anterolateral to oral cavity. Tentoropharyngeal sclerites bridged anterodorsally and with 8–10 ridges ventrally; dorsal cornu heavily pigmented and with a small opening posteriorly; ventral cornu lightly pigmented and bearing a short triangular tooth on dorsal margin; hypopharyngeal sclerite H-shaped and separated from tentoropharyngeal sclerite and mandible; labial sclerite lightly pigmented, extending anteroventrally from and between anterior arms of hypopharyngeal sclerite; parastomal bar projecting anteriorly from tentoropharyngeal sclerite. Mandible strongly curved, lacking accessory teeth, basally with a small opening near ventral margin; small dental sclerite present below base of mandible.

Three thoracic and eight abdominal segments present; anteroventral margin of first thoracic segment with a semiband-like patch of minute spinules; otherwise cuticle bare. Anterior spiracle lightly sclerotized, fan-shaped, with six or seven papillae. Posterior spiracular plate with an ecdysial scar and three oval slits; a pair of minute tubercles present medially on spiracular disc ventral to posterior spiracular plates.

Puparium. About 4.5–6.9 mm long, elongate ovoid in shape, tapering anteriorly with cephalic segment of larva partially invaginated, more bluntly rounded but somewhat flattened posteriorly, pale brownish in color, with larval mouthparts visible through cuticle ventrally. Thoracic segments 2 and 3 with encircling cuticular ridges; those of segment 2 more pronounced. Anterior spiracle with six or seven apical papillae; posterior spiracular disc as in mature larva, but darker in color; anal plate depressed, surrounded by a narrow band of concentric ridges.

Biology and behavior. Little is known about the immature stages of Heleomyzidae. Hennig (1952) summarized the features of known larvae and mentioned that in habitus they do not differ from other saprophagous cyclorrhaphous Diptera larvae. Lobanov (1970) more recently described the larvae of several Holarctic species. Other workers providing descriptions of larvae include Banta (1907), Gorodkov (1963), and Vimmer (1909, 1911). The preceding descriptions of the egg, mature larva, and puparium are of

Pseudoleria crassata Garrett, modified from the descriptions of Garnett and Foote (1967). McAlpine (1984) concluded that *P. crassata* is a junior synonym of *P. placata* (Hutton).

Larvae of Heleomyzidae are found in many types of decaying plant and animal matter (Garnett and Foote 1966, 1967). They are known to occur in bird's nests, mammal burrows, bat caves, carcasses of large mammals, excrement, and fungi. The larvae of the Palaearctic species *Suillia lurida* (Meigen) attacks cultivated onion and garlic plants (Nikolova 1958, Dušek 1963). Adults can be found in moist, shaded woods and around the various larval habitats. Some species are frequently taken indoors.

Classification and distribution. The limits of the family Heleomyzidae were recently redefined (McAlpine 1985). North American workers have generally excluded the Trixoscelididae from the family, although it is sometimes treated as a subfamily. After studying the New Zealand fauna, Harrison (1959) recommended that the family limits be extended to include the Trixoscelididae and that traditional subfamily designations be revised. McAlpine (1967) made the same judgment. In the present work the separation of the Heleomyzidae and the Trixoscelididae is retained for consistency with a previous treatment (Gill 1965). However, two genera, *Neossos* Malloch and *Paraneossos* Wheeler, formerly included with the Trixoscelididae, are now considered to belong with the Heleomyzidae, and following Hennig (1969*a*), the formerly unplaced genus *Cinderella* Steyskal is also assigned to the Heleomyzidae. The inclusion of these three genera makes the previous separation of the subfamilies Suilliinae and Heleomyzinae unfeasible. The designation of new subfamilies within the Heleomyzidae must await a thorough study of the worldwide fauna. McAlpine (1985) classified the family into 22 tribes, of which 12 were newly described. Seven of the 22 tribes are represented in the Nearctic fauna.

Gill (1965) lists 113 species and 23 genera of Heleomyzidae for America north of Mexico. All but the genera *Anorostoma* Loew, *Lutomyia*, *Porsenus* Darlington, and *Pseudoleria* Garrett are Holarctic.

Acceptance of the revisions of the Palaearctic fauna by Gorodkov (1962, 1964, 1965) and the Australian fauna by McAlpine (1985) would eliminate several of the present genera or reduce them to subgeneric status. *Allophyla* Loew is united with *Suillia* in Gorodkov's (1965) and McAlpine's (1985) treatments. *Spanoparea* Czerny is very close to *Morpholeria* Garrett and is considered a subgenus of the latter by Gorodkov (1964) and a synonym by McAlpine (1985). Gorodkov (1963) treated *Trichochlamys* Czerny as a subgenus of *Scoliocentra* Loew, but McAlpine (1985) treated it as a synonym. Griffiths (1972) recently segregated out the genera *Tephrochlamys* Loew and *Heteromyza* Fallén and placed them in the family Heteromyzidae, and he also proposed the family Borboropsidae for the then only known species *Borboropsis puberula* (Zetterstedt), but both of these proposals were rejected by McAlpine (1985). Mathis (1973) raised the possibility that *Oldenbergiella* is not distinct from *Borboropsis*, but McAlpine (1985) recognized both and placed them in two different tribes. None of the above suggested changes has been included in the present work pending further study.

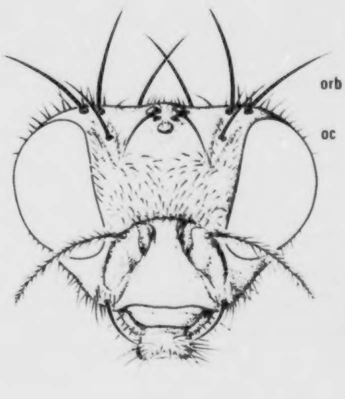
The validity of the assignments of some species to certain genera or their occurrence in North America is also questionable. The present key reflects some of these deviations from previous works (Gill 1962, 1965). Gill (1962, 1965) lists two species of *Allophyla*, but *A. laevis* Loew is no longer considered a distinct species (Gorodkov 1965). *Borboropsis fulviceps* (Strobl), one of the species listed by Mathis (1973) and earlier by Gill (1962, 1965), must be considered a junior synonym of *B. puberula*, according to Hackman and Anderson (1969). Some previous assignments, however, are retained in the following key despite some contrary evidence until further studies are made. *Aecothea fidelis* Curran is treated as a form of *A. fenestralis* (Fallén) by Gorodkov (1959). Thompson and Mathis (1980) indicated that a new name was needed for the group of species formerly included in the genus *Aecothea* of authors, not Haliday. Subsequently Peterson and Gill (1982) proposed the name *Neoecothea* Peterson & Gill to accommodate this group of 3 Nearctic and 11 Palaearctic species, but McAlpine (1985) sank *Neoecothea* as a junior synonym of *Aecothea* Haliday. Gorodkov (1969) stated that *Schroederella iners* (Meigen) is probably incorrectly listed from the Nearctic region and that the correct name for the species should be *luteoala* (Garrett). Finally, the recognition of certain species of *Heleomyza* by Gill (1962, 1965) is probably in error; *H. difficilis* Gill appears to be a junior synonym of *H. maculipennis* (Becker), which Gorodkov (1962) places in the subgenus *Leriola* Gorodkov of the genus *Scoliocentra*.

Thelida Robineau-Desvoidy, now considered a synonym of *Heteromyza* Fallen (McAlpine 1985), is known in North America from fossil evidence only. *Thelida miocenica* (Cockerell) was described (as *Heteromyiella miocenica*) from Miocene shales (Cockerell 1914). Bachofen-Echt (1949) indicated that eight species in three genera were known from Baltic amber, whereas Hennig (1969*b*) listed five species in five genera from these amber deposits.

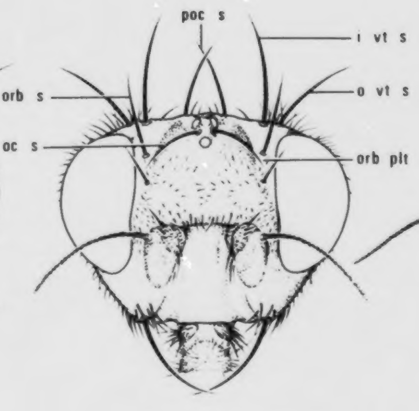
Key to genera

1. Orbital plate oblique, directed inward anteriorly and separated from eye margin (Fig. 2); one orbital bristle on each side. Proepisternal bristle absent. $A_1 + CuA_2$ not reaching wing margin 2

Orbital plate parallel to eye margin, not oblique (Fig. 3). Other characters variable, usually not as described above 4



2 Suillia longipennis ♀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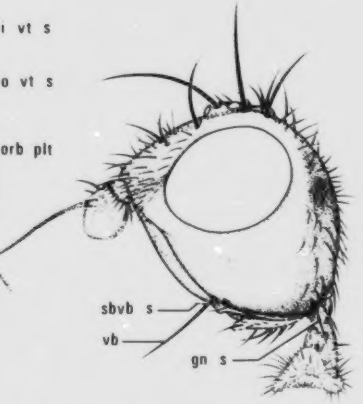
3 Amoebaleria helvola ♀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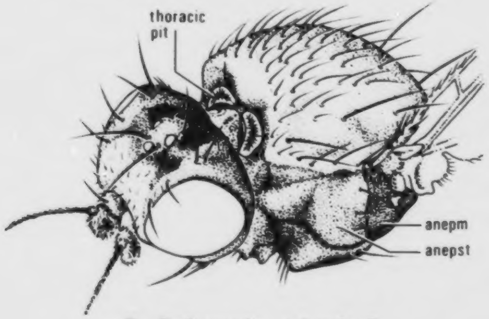
4 Anorostoma coloradense ♀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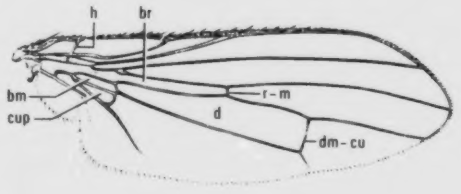
5 Borboropsis puberula ♀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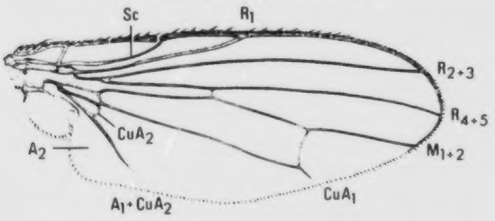
6 Tephrochlamys rufiventris ♀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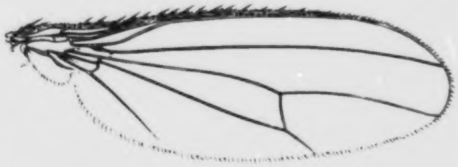
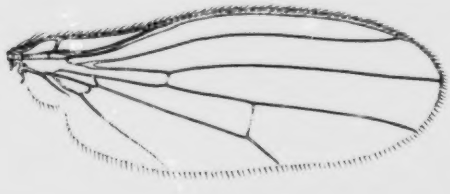
M1+2
A1+CuA2
CuA1

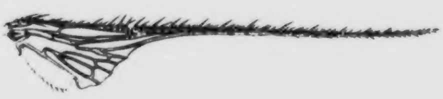
7 Heteromyza oculata ♀



8 Lutomyia spurca ♀



9 Borboropsis puberula ♀



10 Lutomyia hemiptera ♀

Figs. 89.2–10. Heads, thorax, and wings: heads of (2) *Suillia longipennis* (Loew) in anterior view, (3) *Amoebaleria helvola* (Loew) in anterior view, and (4) *Anorostoma coloradense* Garrett in lateral view; (5) head and thorax in anterodorsal view of *Borboropsis puberula* (Zetterstedt); wings of (6) *Tephrochlamys rufiventris* (Meigen), (7) *Heteromyza oculata* Fallén, (8) *Lutomyia spurca* Aldrich, (9) *Borboropsis puberula*, and (10) *Lutomyia hemiptera* (Curran).

Abbreviations: anepm, anepimeron; anepst, anepisternum; gn s, genal bristle; i vt s, inner vertical bristle; oc s, ocellar bristle; orb plt, orbital plate; orb s, orbital bristle; o vt s, outer vertical bristle; poc s, postocellar bristle; sbvb s, subvibrissal bristle; vb, vibrissa.

2. One pair of dorsocentral bristles present .... ***Porsenus*** Darlington

1 sp., *johnsoni* Darlington; known only from type female, Boston, Mass.

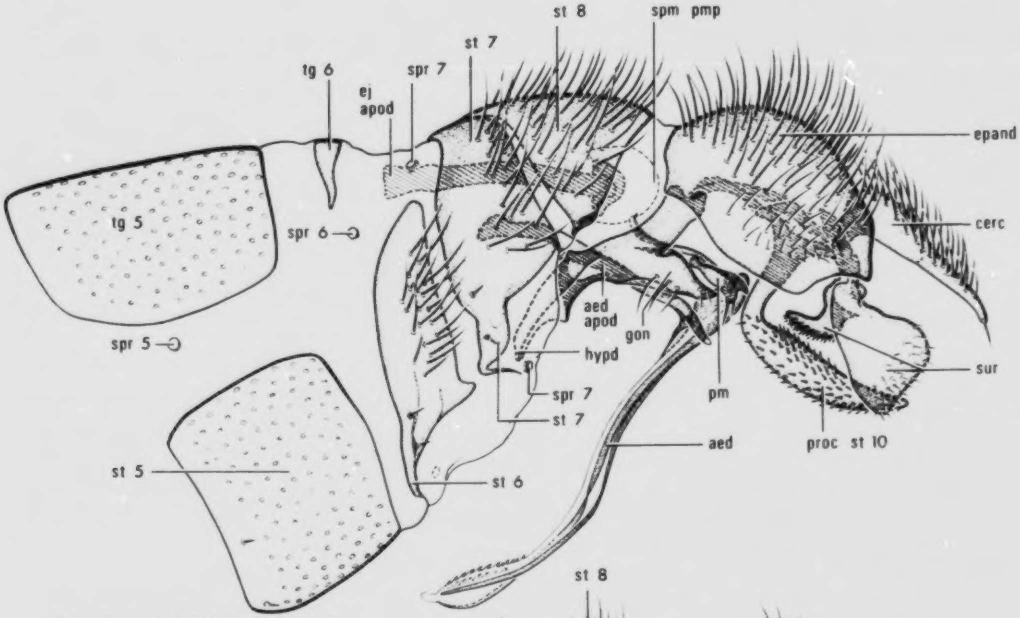
Five pairs of dorsocentral bristles present 3

3. Postpronotal bristle absent .... ***Suillia*** Robineau-Desvoidy

8 spp.; widespread; Gill 1962

Postpronotal bristle present .... ***Allophyla*** Loew

1 sp., *atricornis* (Meigen); widespread; Gill 1962 (=*Suillia*)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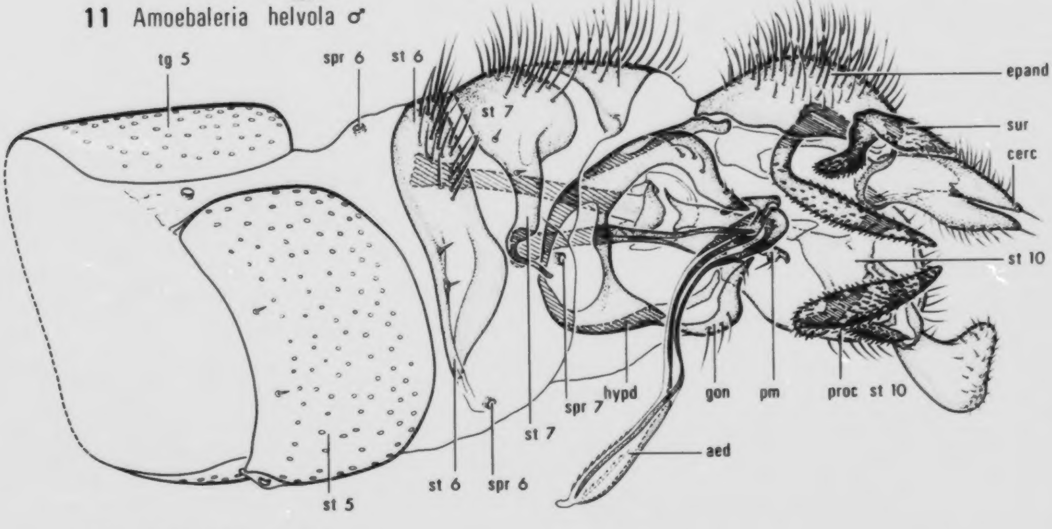
11 Amoebaleria helvola ♂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12 Amoebaleria helvola ♂

Figs. 89.11–12. Male terminalia of *Amoebaleria helvola* (Loew): (11) left lateral view; (12) left ventrolateral view. Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; proc st 10, process of sternite 10; spm pmp, sperm pump; spr, spiracle; st, sternite; sur, surstylus; tg, tergite.

4. Proepisternal bristle absent. $A_1 + CuA_2$ not reaching wing margin. Three orbital bristles on each side in Nearctic species. Body length approximately 2.0 mm 5

Proepisternal bristle present. $A_1 + CuA_2$ reaching wing margin (except in *Neossos*). Usually one or two, but sometimes three, orbital bristles on each side. Body length variable ..6

5. Prominent median facial carina present, protuberant below (Fig. 4.112). Prosternal bristles absent .... ***Cinderella*** Steyskal

1 sp., *lampra* Steyskal; southern U.S.A. northwest to Oregon; Hennig 1969*a*, Steyskal 1969

Prominent facial carina lacking. Prosternal bristles present .... ***Paraneossos*** Wheeler

1 sp., *arizonicus* Wheeler; Arizona; Wheeler 1955

6. Body length less than 3.0 mm. Costal spines of wing absent or small. Preapical dorsal bristles of tibiae (in Nearctic species) poorly developed, sometimes distinct on hind tibia only....7

Body length usually greater than 3.0 mm. Costal spines of wing well-developed. Preapical dorsal bristles of tibiae well-developed 8

7. Posterior portion of anepisternum with bristle. Thoracic pits present (Fig. 5) .... ***Borboropsis*** Czerny

2 spp.; northwestern U.S.A., Canada; Mathis 1973

Posterior portion of anepisternum bare. Thoracic pits absent .... ***Oldenbergiella*** Czerny

1 sp., *brumalis* Czerny; Manitoba; Gill 1962

8. Prosternal bristles absent...9

Prosternal bristles present 22

9. Mid tibia with one apical ventral bristle 10

Mid tibia with several apical ventral bristles 11

10. R_1 ending at or near level of crossvein r-m (Fig. 6)............... ***Tephrochlamys*** Loew

2 spp.; widespread; Gill 1962

R_1 ending distinctly beyond level of crossvein r-m (Fig. 7) .... ***Heteromyza*** Fallén

1 sp., *oculata* Fallén; Canada, Alaska; Gill 1962

11. More than four pairs of dorsocentral bristles usually evident; three lateral scutellar bristles present on each side .... ***Orbellia*** Robineau-Desvoidy

3 spp.; widespread; Gill 1962

Four or fewer pairs of dorsocentral bristles present, with the anteriormost sometimes weakened; two lateral scutellar bristles present on each side 12

12. Crossvein r-m situated at or before basal fourth of cell dm; R_{2+3} lying almost parallel to R_1 and contacting C near union of R_1 with C (Figs. 8, 10); wing sometimes mutilated (Fig. 10) .... ***Lutomyia*** Aldrich

4 spp.; widespread; Sabrosky 1949

Crossvein r-m situated near or beyond middle of cell dm; R_{2+3} diverging from R_1 and joining C far beyond union of R_1 with C (Figs. 6, 7); wing usually intact 13

13. Mid tibia with several bristles well before apex on anterodorsal and posterodorsal surfaces .... ***Aecothea*** Haliday

3 spp.; widespread; Gill 1962

Mid tibia without bristles, except near apex 14

14. Mid femur with rows of bristles anteriorly .... ***Eccoptomera*** Loew

7 spp.; Iowa and Saskatchewan west to British Columbia and California; Gill 1962

Mid femur without rows of bristles anteriorly 15

15. Anepimeron with hairs or bristles .... ***Pseudoleria*** Garrett

12 spp.; widespread; Gill 1962

Anepimeron bare 16

16. Anepisternum with one or more bristles posteriorly. Face receding below; eye horizontally oval (Fig. 4)... ***Anorostoma*** Loew

16 spp.; widespread; Gill 1962

Anepisternum bare. Face usually not markedly receding below; eye round or nearly so....17

17. Anterior and posterior orbital bristles approximately equal in length..................18

Anterior orbital bristle shorter than posterior bristle 19

18. $A_1 + CuA_2$ not reaching wing margin .... ***Neossos*** Malloch
    2 spp.; widespread; Melander 1952
    $A_1 + CuA_2$ reaching wing margin .... ***Neoleria*** Malloch
    8 spp.; northern U.S.A., Canada; Gill 1962

19. Arista short, less than three times length of first flagellomere 20
    Arista long, greater than three times length of first flagellomere 21

20. Arista bare or minutely pubescent. Body mostly blackish in Nearctic species ....
    .... ***Morpholeria*** Garrett
    1 sp., *tristis* (Loew); Canada, Alaska; Gill 1962
    Arista clearly pubescent. Body mostly yellow in Nearctic species ..... ***Spanoparea*** Czerny
    2 or 3 spp.; northern U.S.A., Canada; Gill 1962 (possibly =*Morpholeria*)

21. Katepisternum with one bristle .... ***Acantholeria*** Garrett
    3 spp.; western U.S.A. and Canada; Gill 1962
    Katepisternum with two (rarely three) bristles .... ***Schroederella*** Enderlein
    2 spp.; widespread; Gill 1962

22. Prosternum with one (rarely two or three) pair of bristles; if more than one pair of prosternal bristles present, then anterior orbital bristle distinctly shorter than posterior bristle...23
    Prosternum with two or more pairs of bristles. Anterior and posterior orbital bristles approximately equal in length 25

23. Anepimeron haired .... ***Scoliocentra*** Loew
    3 spp.; northern U.S.A., Canada; Gill 1962
    Anepimeron bare 24

24. Anterior orbital bristle shorter than posterior orbital bristle .... ***Amoebaleria*** Garrett
    15 spp., including two European species for which Nearctic records are questionable; widespread; Gill 1962 (possibly =*Scoliocentra* Loew)
    Orbital bristles approximately equal in length .... ***Anypotacta*** Czerny
    2 spp.; western; Gill 1962

25. Scutellum bare on dorsum; anepimeron bare, except in *maculipennis* (Becker) ....
    .... ***Heleomyza*** Fallén
    9 spp.; widespread; Gill 1962
    Scutellum setose dorsally; anepimeron haired .... ***Trichochlamys*** Czerny
    1 sp., *borealis* Czerny; Alaska, Bering Strait; Gill 1962 (possibly =*Scoliocentra* Loew)

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TRIXOSCELIDIDAE

90

H. J. TESKEY

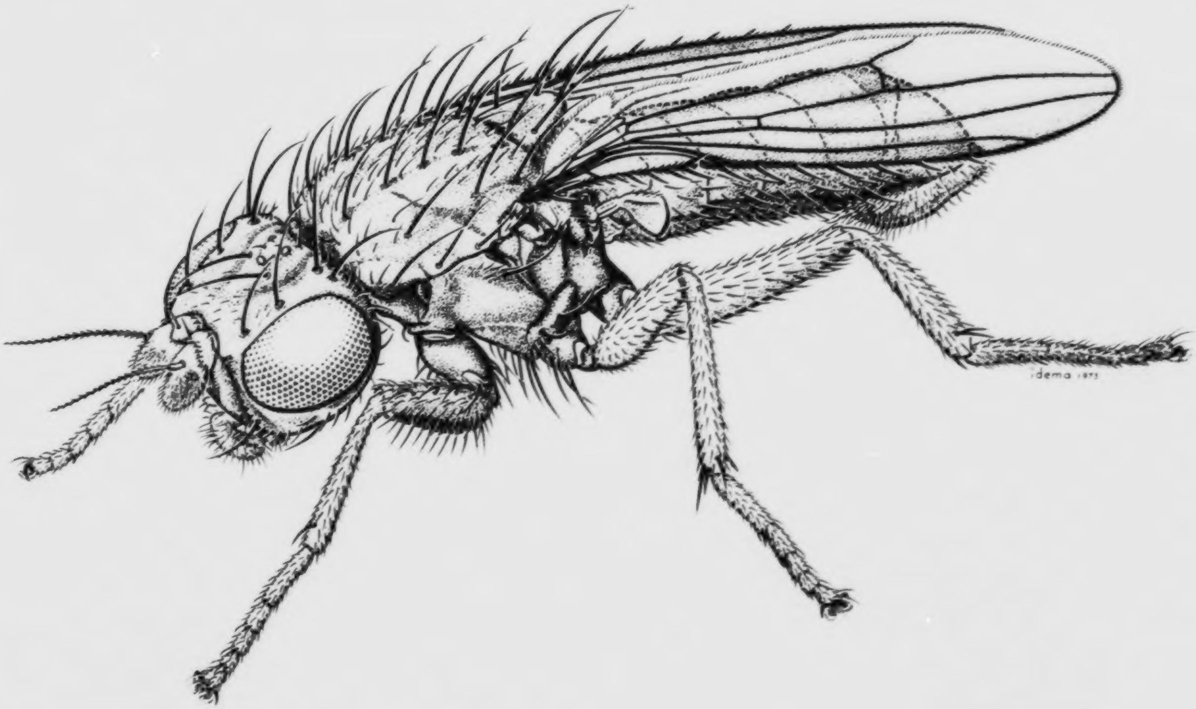


Fig. 90.1. Male of *Trixoscelis fumipennis* Melander.

Small flies (Fig. 1), 1.5–3 mm long, predominantly pruinose. Abdomen sometimes glabrous. Legs, face, antennae, and portion of frons, and in one genus (*Zagonia* Coquillett) entire body, yellow. Wing hyaline, sometimes with infuscation along veins and crossveins, or mostly blackened with conspicuous hyaline spots.

Adult. Head: about as wide as thorax, wider than high, usually higher than long (Fig. 1); greatest length at level of antennae. Eye nearly round, bare. Frons equal to or wider than high in both sexes, widened above; lower half or more usually yellow to orange. Face usually slightly concave. Gena 0.1–0.4 as wide as head height. Frons with two reclinate orbital bristles and sometimes with sparse fine setulae on lower half; ocellar and inner and outer vertical bristles strong; ocellar bristles situated beside anterior ocellus, but laterally to margins of ocellar triangle; ocellar triangle with one or more pairs of small setulae; postocellar bristles rather small, convergent; paravertical bristles often present, small; vibrissa well-developed; a single row of subvibrissal setae usually present on gena, of which foremost one or two may be enlarged; one or two genal bristles usually present; postocular fringe consisting of a single row of setae between outer vertical bristle and genal bristles; supracervical patches of setae and scattered setae present on occiput. Scape small, often hidden within antennal socket; pedicel with apical fringe of incumbent bristles and porrect dorsal bristle; first flagellomere oblong to nearly round, with dorsobasal pubescent arista. Proboscis rather short, pale, with membranous labella; palpus slender, clavate, with one or more apical bristles.

Thorax: often gray, sometimes with brownish longitudinal stripes on scutum and upper margin of pleura, or with brown spots at base of bristles, or with both types of markings; prosternum small, well-separated from propleuron. Chaetotaxy: mesonotum with one postpronotal bristle and sometimes associated setae, two notopleural bristles, a presutural and postsutural supra-alar bristle, two postalar bristles, five dorsocentral bristles (two of which are presutural), and two to four rows of acrostichal setae of which prescutellar setae are sometimes slightly enlarged; scutellum with two pairs of marginal bristles, and with disc bare; propleural bristle weak or strong; proepimeral seta often absent; anepisternum with a bristle and one to several adjacent setulae; katepisternum with two strong bristles dorsally and several bristles and setulae ventrally; other pleural sclerites bare; prosternum sometimes with one or two pairs of setae.

Wing (Figs. 1, 3) moderately broad, with well-developed anal lobe and alula. C extending to end of M_{1+2}, broken only at end of Sc, and usually with conspicuous spines among costal setulae; Sc complete and free from R_1, and ending in C very near R_1 near basal third of wing; R_{2+3} ending in apical fifth of wing; R_{4+5} and M_{1+2} ending near wing apex; cell dm long, separated from cell bm by a crossvein; cell cu*p* closed; A_1 extending one-half to two-thirds distance from cell cu*p* to wing margin. Calypteres small; lower one linear. Halter yellow.

Legs, although predominantly yellow, usually with fore femur and sometimes all of foreleg darkened. Femora slightly swollen (Fig. 1); fore femur darker than others; strong bristles lacking, although rows of setae enlarged dorsally and ventrally on posterior face of fore femur and sometimes on anterior face near apex of mid and hind femora. Tibiae with preapical dorsal bristles; mid tibia with one or more apicoventral bristles.

Abdomen: setulose (Fig. 1), with row of setae longer posteriorly on tergites than elsewhere, usually gray or yellow pruinose, sometimes glabrous, or with conspicuous dark brown mottled pattern. Six abdominal spiracles present in both sexes.

Male terminalia (Fig. 4) with pregenital sclerites asymmetric. Tergite 6 slender, separated from partially fused syntergosternite 7 + 8. Cercus and surstylus usually present; surstylus lacking only in *Zagonia*; cercus in form of small setiferous lobe; surstylus large, often tapered to a long point, and usually appearing flexibly articulated to epandrium. Gonopod and paramere usually well-developed, of greatly varied form; aedeagus varied and complex; distiphallus often trifid, with one or more of the three parts ribbon-like; all parts of distiphallus equal in length and spoon-shaped in *Zagonia*, but in other taxa one part dominant.

Female with three spermathecae. Ovipositor short and abruptly tapered from segment 7 in Nearctic species (Fig. 5), but fairly long and telescoped in some Palaearctic species of *Trixoscelis* Rondani. Tergite 7 and sternite 7 fused when ovipositor short. Sternite 8 with lateral setaceous lobes in *Trixoscelis* and *Spilochroa* Williston. Epiproct, hypoproct, and small cerci distinct.

Biology and behavior. Nothing is known of the immature stages or the biology of the group. Adults are frequently collected on flowers and vegetation. The fact that most species are confined to the western part of the continent, many in arid states, undoubtedly has some biological significance.

Classification and distribution. The limits of the family are reasonably distinct in the Holarctic region, but elsewhere, as pointed out by Gill (1962) and others, the difficulty of maintaining a distinction from the Heleomyzidae appears insurmountable. Cogan (1971) found it necessary to combine the two families in the Ethiopian region, although later (Cogan 1977), following Griffiths (1972), he recognized the possible validity of the family. McAlpine (1985) has also included the Trixoscelididae in the Heleomyzidae, although he still recognizes it as one of 22 world tribes. In conformity with the treatment of the group (Vockeroth 1965) in the *Catalog of North American Diptera*, separate family status is retained for the Nearctic fauna. McAlpine (1985) included the monotypic Palaearctic genera *Paratrixoscelis* Soós and *Psiloplogia* Czerny in his tribe Trixoscelidini. In addition to the three Nearctic genera recognized in the key below, the family is usually considered to include *Stuckenbergiella* Cogan, a monotypic Ethiopian genus, and *Neossos* Malloch and *Paraneossos* Wheeler, two Nearctic genera with two and one species, respectively. However, study here and by McAlpine (1985) has shown that both *Neossos* and *Paraneossos* are more closely related to the Heleomyzidae than to the genera assigned to the Trixoscelididae. For example, *Paraneossos* is very similar to *Cephodapedon* Malloch, a Neotropical heleomyzid genus. Cogan (1977) also referred *Neossos* to the Heleomyzidae. Therefore, these latter two genera are not considered here to belong to the Trixoscelididae. Cogan (1977) synonymized *Spilochroa* with *Trixoscelis*, although he agreed that the *Spilochroa* group of species is probably monophyletic. McAlpine (1985) synonymized both *Zagonia* and *Spilochroa* under *Trixoscelis*. However, because the Nearctic species of both *Spilochroa* and *Zagonia* have a rather distinctive appearance, the genera are provisionally retained here.

The family has not been reported from the Oriental and Australian regions. In the Palaearctic and Ethiopian regions it is represented almost solely by *Trixoscelis*, with 13 and 22 species recognized, respectively. Four species of *Trixoscelis* and three of *Spilochroa* have been recorded from the Neotropical region, but two species of each genus are also present in the Nearctic region. No fossil representatives of the family are known.

Figs. 90.2–5. Head, wing, and terminalia: (2) head of *Zagonia flavicornis* Melander; (3) wing of *Spilochroa ornata* (Johnson); (4) left lateral view of male terminalia of *Trixoscelis frontalis* (Fallén); (5) left lateral view of female terminalia of *Trixoscelis frontalis*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; hypd, hypandrium; hyprct, hypoproct; i vt s, inner vertical bristle; oc s, ocellar bristle; orb s, orbital bristle; o vt s, outer vertical bristle; pm, paramere; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; vb, vibrissa.

⇨

Key to genera

1. Body entirely or predominantly yellow. Gena at least one-half as wide as height of eye in lateral view (Fig. 2) .... ***Zagonia*** **Coquillett**

   2 spp.; western; Melander 1952

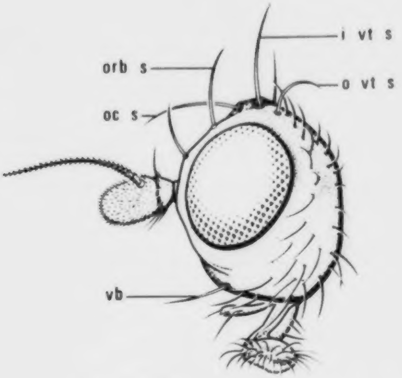
   Body predominantly gray, with yellow coloration restricted to head and legs. Gena narrower than one-half height of eye 2

2. Wing dark, with hyaline spots (Fig. 3). Gena no more than one-eighth as wide as height of head. Hind femur with an enlarged anterior subapical bristle ...... ***Spilochroa*** **Williston**

   5 spp.; southwest; Wheeler 1955

   Wing hyaline, or with infuscation along veins or bordering crossveins, or both (Fig. 1). Gena up to one-third as wide as height of head. Hind femur without a distinct anterior subapical bristle .... ***Trixoscelis*** **Rondani**

   20 spp.; predominantly western; Melander 1952



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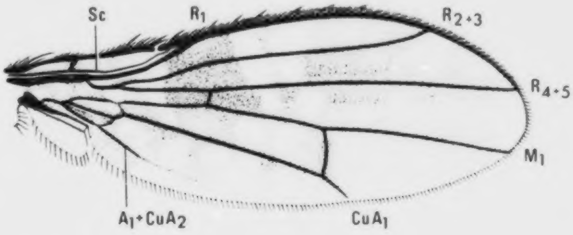
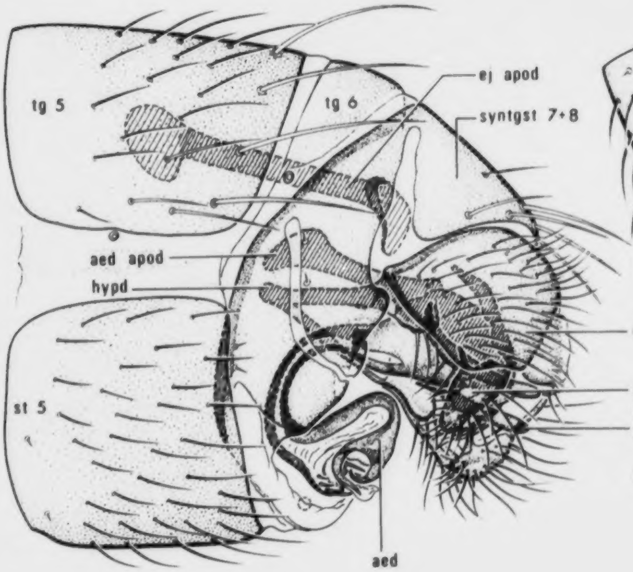
2 Zagonia flavicornis ♂



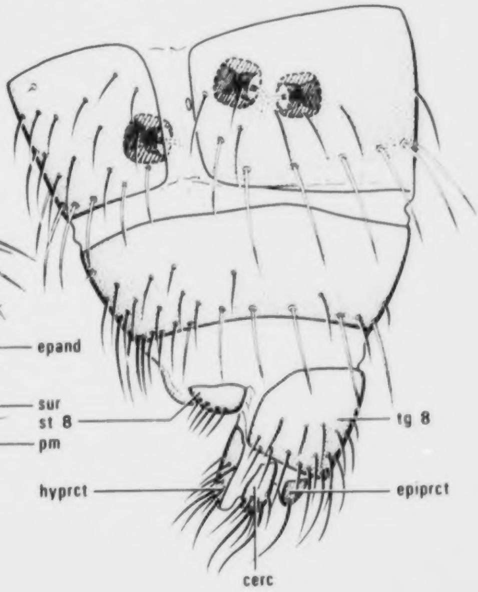
Sc
R1
R2+3
R4+5
M1
A1+CuA2
CuA1

3 Spilochroa ornata ♀



tg 5
tg 6
ej apod
syntgst 7+8
aed apod
hypd
epand
st 5
sur
st 8
pm
aed

4 Trixoscelis frontalis ♂



tg 8
hyprct
epiprct
cerc

5 Trixoscelis frontalis ♀

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CHYROMYIDAE

91

J. F. McAlpine

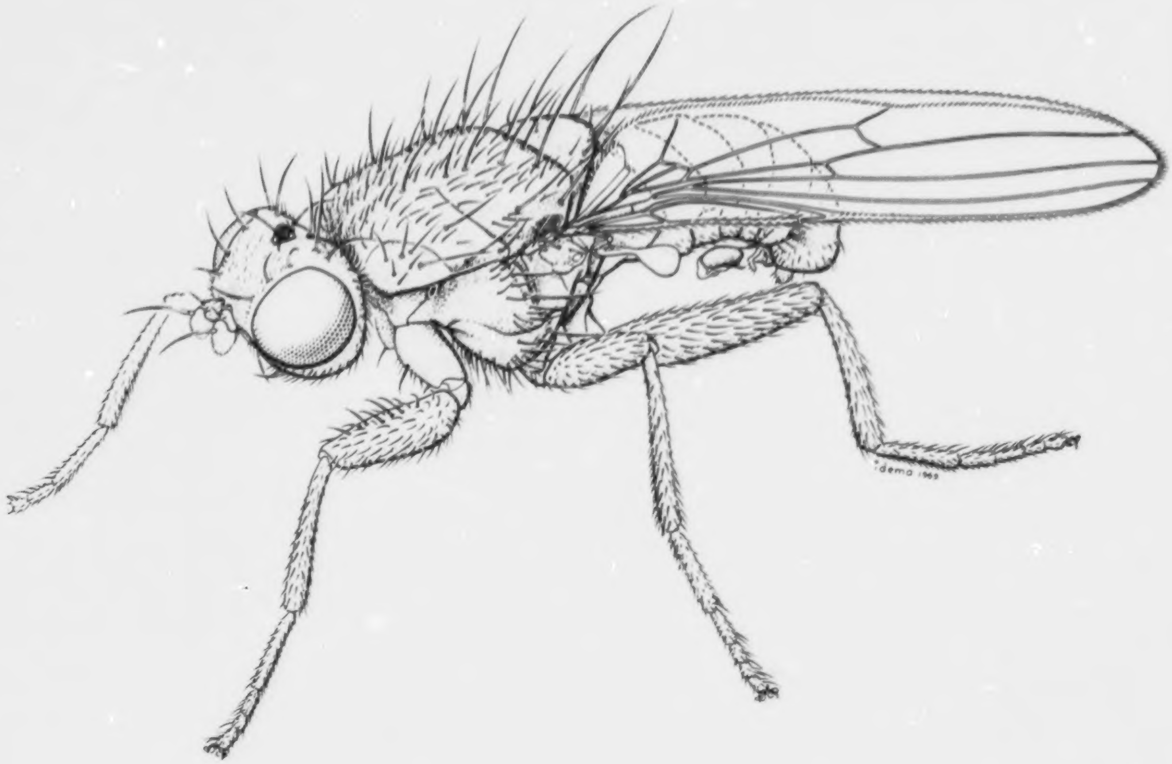
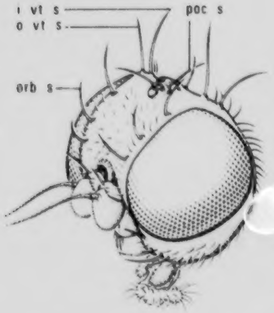


Fig. 91.1. Adult male of *Chyromya flava* (Linnaeus).

Small to very small drosophilid-like flies (Fig. 1), 1.0–4.5 mm long, usually yellowish in color with yellowish bristles and hairs and clear wings.

Adult. Head: with frons narrowed anteriorly (Figs. 2–4); fronto-orbital plate extending almost to anterior border of frons; two or three fronto-orbital bristles usually present, (absent in *Aphaniosoma aldrichi* Wheeler); interfrontal area weakly sclerotized, weakly to strongly setulose; ocellar and inner and outer vertical bristles usually relatively strong; postocellar bristles usually present, convergent; lunule small, largely unexposed. Face depressed, desclerotized in middle; facial carina usually absent, but fairly strongly developed in *Aphaniosoma* Becker. Gena rather broad, mostly short-haired; vibrissal angles often encroaching on face; vibrissae rather weak, sometimes scarcely distinguishable from subvibrissal setae and similar setulae above vibrissa. Antenna short; first flagellomere reniform; arista microscopically pubescent. Proboscis short and fleshy; palpus unusually small.

Thorax: usually entirely pale yellow, with yellow bristles and hairs: one posteriorly directed outer and usually one inwardly directed inner postpronotal, one presutural supra-alar, two notopleural, and one or two postsutural supra-alar bristles present; presutural dorsocentral bristles present or absent; one to four postsutural dorsocentral bristles present; acrostichal setulae arranged in two to ten rows; postsutural acrostichal bristles present or absent; scutellum with four bristles, frequently with additional setulae. Proepisternal bristle absent except in some species of *Aphaniosoma*; proepimeral bristle absent. Anepisternum posteriorly with one bristle and a few setulae; katepisternum usually with one strong bristle and additional setulae (bristle absent in *Aphaniosoma*); anepimeron bare. Prosternum very narrow and with deep median groove. Wing (Fig. 5) moderately broad, with well-developed anal lobe and alula; C extending to M_1, with anterior spines reduced or absent, and with a subcostal break; Sc complete, but weak on apical fifth, and joining C very close to insertion of R_1; cells dm and bm separated by a crossvein; cell cu*p* present; A_1 present, ex-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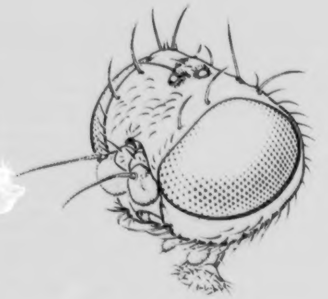
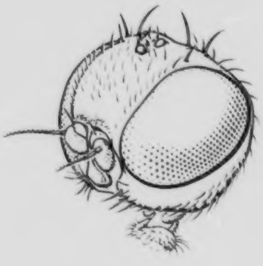
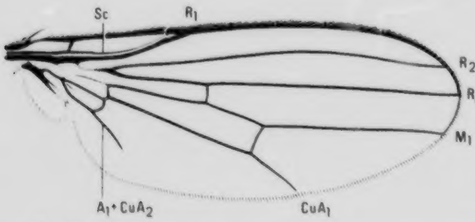
2 Gymnochiromyia concolor ♀



3 Aphaniosoma quadrivittatum ♀



4 Aphaniosoma aldrichi ♀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R4+5
M1
A1+CuA2
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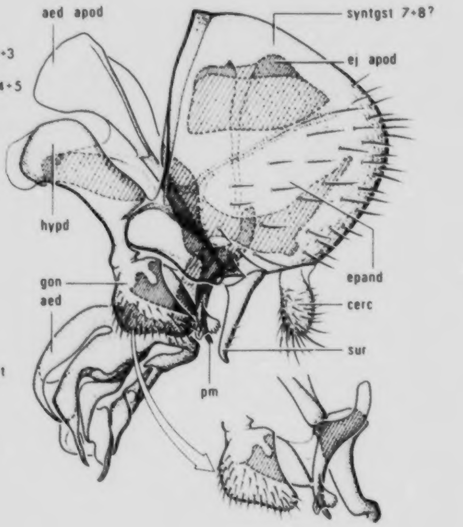
5 Chyromya flava ♂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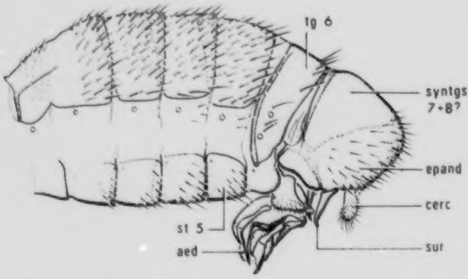
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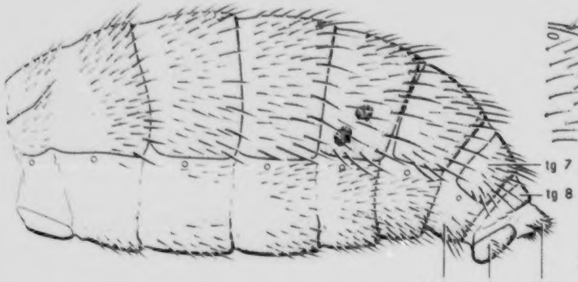
6 Chyromya flava ♂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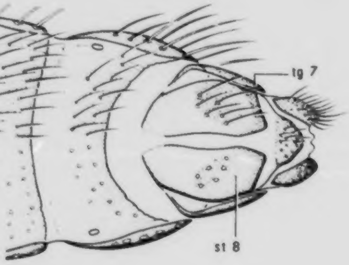
8 Chyromya flava ♀



9 Chyromya flava ♀

Figs. 91.2-9. Heads, wing, and terminalia: heads of (2) *Gymnochiromyia concolor* (Malloch), (3) *Aphaniosoma quadrivittatum* Malloch, and (4) *Aphaniosoma aldrichi* Wheeler; (5) wing of *Chyromya flava* (Linnaeus); (6) abdomen and (7) terminalia of male of *Chyromya flava*, left lateral view; (8) abdomen and (9) terminalia of female of *Chyromya flava*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; i vt s, inner vertical seta; orb s, orbital seta; o vt s, outer vertical seta; pm, paramere; poc s, postocellar seta; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

tending about three-fourths of distance to wing margin. Legs weakly bristled; front and hind femora frequently enlarged in male; all tibiae without a dorsal preapical bristle; ventral bristles at apex of mid tibia short.

Abdomen: male (Figs. 6, 7) with tergite 6 reduced and syntergosternite 7 + 8 fused with epandrium. Spiracles 6 and 7 enclosed in tergite 6. Epandrium, hypandrium, and associated structures symmetric. Cercus small and fleshy. Surstylus articulated to posteroventral angle of epandrium, varying greatly in form. Hypandrium short; gonopod with rather strong bristles; paramere slender and with a cluster of fine setulae near apex; aedeagus short and stout; basiphallus apparently without an epiphallus; distiphallus very complex; aedeagal apodeme short, extensively fused with hypandrium; ejaculatory apodeme very short and broad, more or less umbrella-like (Fig. 7).

Abdomen of gravid females often much distended and swollen, with outline of eggs clearly evident in dried specimens; abdominal tergites and sternites 1–7 of female well-developed (Figs. 8, 9); six or seven spiracles present in membrane. Female terminalia forming a short tubular ovipositor; tergite 8 and sternite 8 not fused; sternite 8 divided, at least in *Chyromya* Robineau-Desvoidy; cerci short, separate, not heavily sclerotized; two sclerotized spermathecae present, subspherical, frequently visible through body wall as two dark subapical dorsal spots.

Biology and behavior. The larvae and pupae are unknown. Adults of *Chyromya* and *Gymnochiromyia* Hendel have been reared from bird's nests and from the wood debris of hollow trees (Collin 1933). Adult females are frequently found in windows; both sexes are sometimes swept from foliage of shrubs and herbage, especially around the margins of creeks and ponds. *Aphaniosoma* appears to frequent grasses and sedges on seashores and around alkaline or saline ponds or lakes.

Classification and distribution. The family consists of three genera, *Chyromya*, *Gymnochiromyia*, and *Aphaniosoma*, all of which occur in the Holarctic, Ethiopian, and Oriental-Papuan regions; 15 of about 40 known species occur in North America. The genus *Chyromya* has many synonyms and misspellings, most of which were summarized by Malloch (1914); Frey's (1958) subgenus *Somatiosoma* (type, *Chyromya* (*Somatiosoma*) *nitescens* Frey, from the Cape Verde Islands) is probably an additional synonym. The three species of *Chyromya* that occur in the Nearctic region also occur in the Palaearctic region. About six Nearctic species of *Gymnochiromyia*, four of which are undescribed, are known in North America; the same is true of *Aphaniosoma*. One fossil species, *Gephromyiella electrica* Hennig from Baltic amber (Hennig 1965, 1969), was doubtfully placed in the family; it differs from all extant Chyromyidae in having body integument and bristles dark, second aristomere elongate, vibrissa strongly developed, palpi relatively large, both a proepisternal and a proepimeral bristle present, and vein A_1 reaching the wing margin; in addition it is described as not having a subcostal break in C. In the light of these and other differences, I consider it unlikely that it belongs to the Chyromyidae. More study of all known specimens (Hennig 1969) is needed to clarify its relationships.

The following features are judged to be autapomorphic characters of the Chyromyidae: integument and vestiture extensively pale yellow, face broadly desclerotized in the middle, vibrissal angles displaced upward and inward, vibrissa reduced and displaced downward to a subvibrissal position, palpi and mouthparts small, costal spines secondarily reduced, preapical dorsal tibial bristles secondarily reduced or absent, tergite 6 of male secondarily symmetric, surstylus more or less fused with epandrium, ejaculatory apodeme umbrella-shaped, and only two spermathecae present.

The Chyromyidae are closely related to the Heleomyzidae. It agrees with that family in having convergent postocellar bristles, a subcostal break in C, costal spines sometimes present, and a reduced abdominal tergite 6 in the male. Within the Heleomyzidae, the genus *Cephodapedon* Malloch shares the following peculiarities with Chyromyidae: three strong orbital bristles present with the anterior one tending to be inclinate, a very narrow prosternum, enlarged front and hind femora in the male, and only two spermathecae present in the female.

At the same time, however, the Chyromyidae share the following peculiarities with the Sphaeroceridae: a very narrow prosternum with a deep median groove, an inwardly directed inner postpronotal bristle present, apical portion of Sc lying very close to or joining R_1, A_1 not reaching the wing margin, spiracles 6 and 7 of the male situated in tergite 6, syntergosternite 7 + 8 of the male united with epandrium and with the two parts secondarily symmetric, aedeagus short and stout and with a very complex distiphallus, and sternite 8 of the female divided or otherwise modified. These conditions indicate that Chyromyidae and Sphaeroceridae are sister groups, a possibility that was first advanced by Griffiths (1972).

Key to genera

1. Scutellum with two to twelve discal setulae, in addition to four marginal scutellar bristles .... ***Chyromya*** Robineau-Desvoidy

3 spp.; widespread, Holarctic; Malloch 1914

Scutellum with four to six marginal scutellar bristles only 2

2. Frons with three pairs of strong orbital bristles, the anterior pair incurved. Proepisternal bristle absent. Face without a keel .... ***Gymnochiromyia*** Hendel

3 spp.; widespread; Malloch 1914

Frons usually with two pairs of strong orbital bristles (absent in *A. aldrichi*), the anterior incurved pair always absent. Proepisternal bristle present, though small. Face usually with a complete median keel .... ***Aphaniosoma*** Becker
3 spp.; widespread; Wheeler 1961

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RHINOTORIDAE

92

J. F. McAlpine

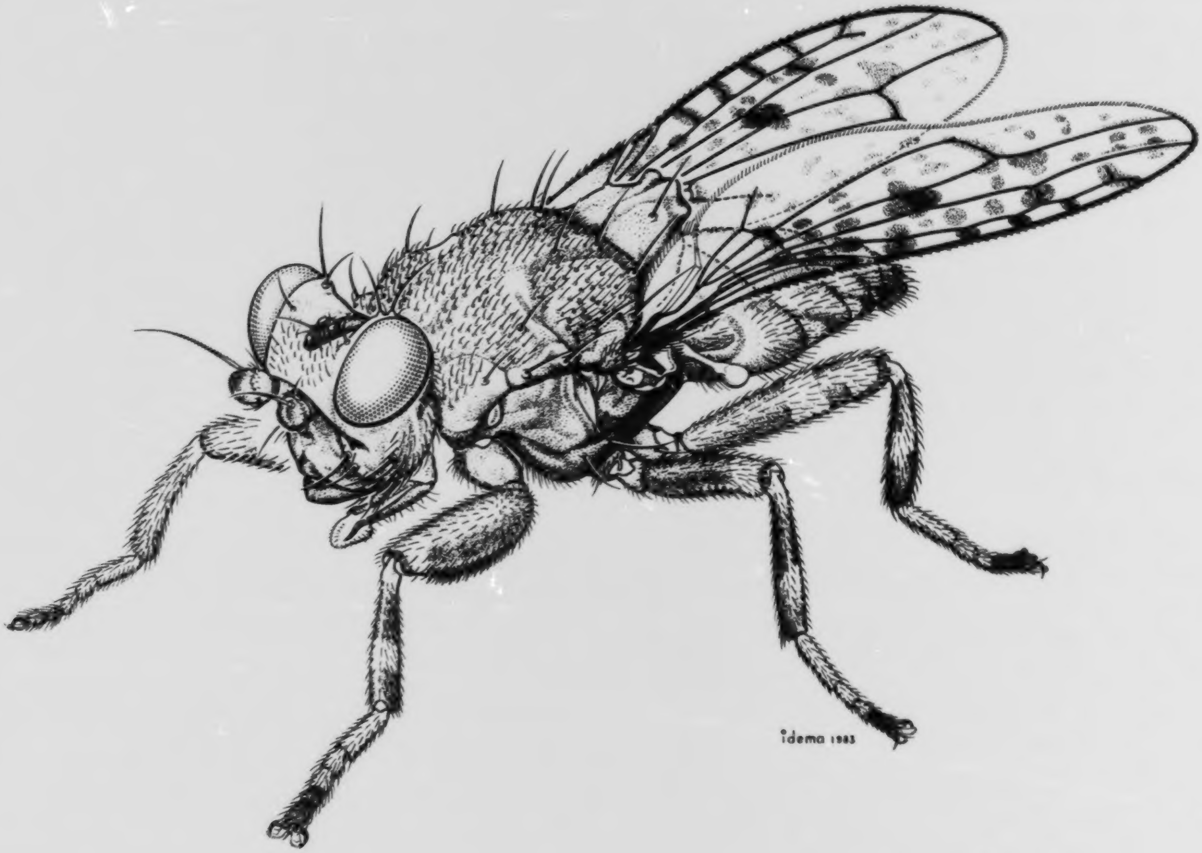


Fig. 92.1. Adult male of *Neorhinotora diversa* (Giglio-Tos).

Medium-sized sciomyzid-like flies (Fig. 1), about 6 mm long, with mottled wings, deeply excavated vertex, and stout femora.

Adult. Head: nearly twice as high as long, somewhat triangular in front view, with vertex strongly concave and upper margins of eyes prominently projecting (Fig. 2). Frons distinctly narrower at lunule than at anterior ocellus, with very fine and rather sparse setulae; one or two reclinate orbital bristles present; inner and outer vertical bristles strong; postocellar bristles usually absent, but weakly present and convergent in *Rhinotoroides* Lopes and *Cairnsimyia* Malloch; ocellar bristles strong to weak; lunule small, with transverse upper margin. Face long, strongly concave in lateral view, without median carina or antennal grooves, frequently with a dark transverse band in middle. Cheek very broad, occupying one-half or more of side of head; vibrissa located about halfway between subcranial margin and lower margin of eye; subgenal bristle strong, about equal to vibrissa in size; clypeus broad and prominent. Compound eye elongately oval, nearly twice as long as high in lateral view, with a bulging appearance above, bare. Antenna short and porrect; pedicel without a seam or notch, not swollen above; first flagellomere oval; arista bare to shortly pubescent. Distal section of proboscis elongate, with rather small labella; palpus of ordinary size and shape.

Thorax: with variegated gold, gray, and brown pruinescence, usually with a conspicuous dark brown pleural stripe running from in front of anterior spiracle to base of wing (Fig. 1). Scutum with rather sparse short decumbent setulae; one postpronotal, one presutural intra-alar, two notopleural, two supra-alar, one postsutural intra-alar, and one or two dorsocentral bristles present; scutellum more or less flattened above, bare or hairy, with two pairs of bristles, with (*Rhinotora* Schiner) or without lateral and apical spurs

(Fig. 4); prescutellum undeveloped; subscutellum weakly developed. Disc of propleuron haired or bare; proepisternal and proepimeral bristles very weak or absent; anepisternum usually bare, sometimes with hairs or weak posterior bristles or both; katepisternum haired, and with one to three bristles; remaining pleural sclerites bare. Prosternum small and narrow, free from propleuron, and usually bare, but haired in *Cairnsimyia*; metasternal area bare.

Wing (Fig. 3) extensively patterned with brown spots, with a varying number of supernumerary crossveins between C and R$_{2+3}$, except in *Cairnsimyia*. C broken at apex of Sc, usually without spines; Sc obsolete at extreme apex, except in *Cairnsimyia*; apex of R$_1$ close to apex of Sc; CuA$_1$ and A$_1$ not reaching wing margin; cell cu*p* well-developed; cell dm large, with crossvein r-m meeting it near middle. Calypteres small; lower lobe linear. Halter normal, entirely whitish.

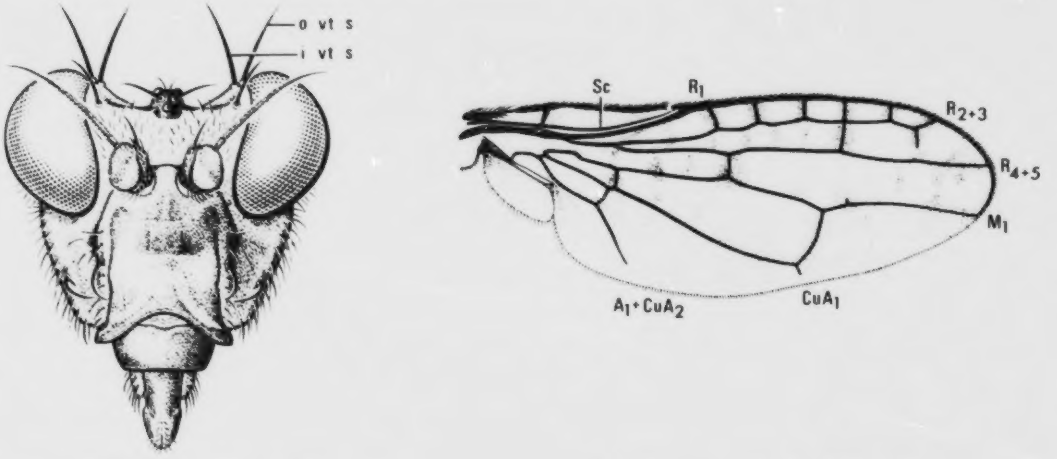
Legs stocky (Fig. 1). Femora heavily developed; fore femur, at least, usually with a series of stout bristles on ventral surface. Tibiae usually banded; preapical dorsal bristles weak or absent. Tarsomere 1 of hind tarsus shortened in males of some forms, e.g. *Cairnsimyia excavata* D. K. McAlpine.

Abdomen: short and broad (Figs. 1, 5, 7), with seven pairs of spiracles. Male (Figs. 5, 6) with tergite 6 much reduced to almost obliterated, but when present usually fused with remnants of segments 7 and 8; sternite 5 sometimes with posterolateral margins modified as specialized lobes (*Rhinotora*); sternites 6 and 7 reduced to narrow sclerites in left side, partially fused together and thence with remnants of segment 8, usually preceded by a narrow secondary band that traverses ventral surface and forms anterolateral margin of large consolidated dorsal sclerite (remnants of segments 6 + 7 + 8); spiracles 6 and 7 enclosed in sides of consolidated sclerite. Epandrium large and fully exposed, without strong bristles. Surstylus large and pendulant, freely articulated with epandrium, frequently consisting of an outer posterior and an inner anterior lobe; inner surface frequently densely setulose, but without true prensisetae. Cerci usually fused and joined to posterior margin of epandrium, except in *Cairnsimyia* where they are free or fused but free from epandrium. Hypandrium short and weak; gonopod in form of a raised lobe bearing fairly strong bristles on its apical margin; paramere elongate (*Neorhinotora* Lopes) to very short (*Rhinotora*); aedeagus short with simple to complex distiphallus; epiphallus indistinct or absent; aedeagal apodeme weakly developed, more or less fused with hypandrium; ejaculatory apodeme small.

Female terminalia (Figs. 7, 8) with ovipositor short and stout, not adapted for piercing. Sternite 7 and tergite 7 free to partially fused at sides; spiracles 6 and 7 situated in membrane. Cerci free from each other, with numerous setulae and hairs. Two spermathecae present, spherical, heavily sclerotized, smooth.

Larva. Immature stages of New World genera unknown. D. K. McAlpine (1968) described and illustrated the last-stage larva of one Australian species, *Cairnsimyia robusta* (Walker); the following description is based on it.

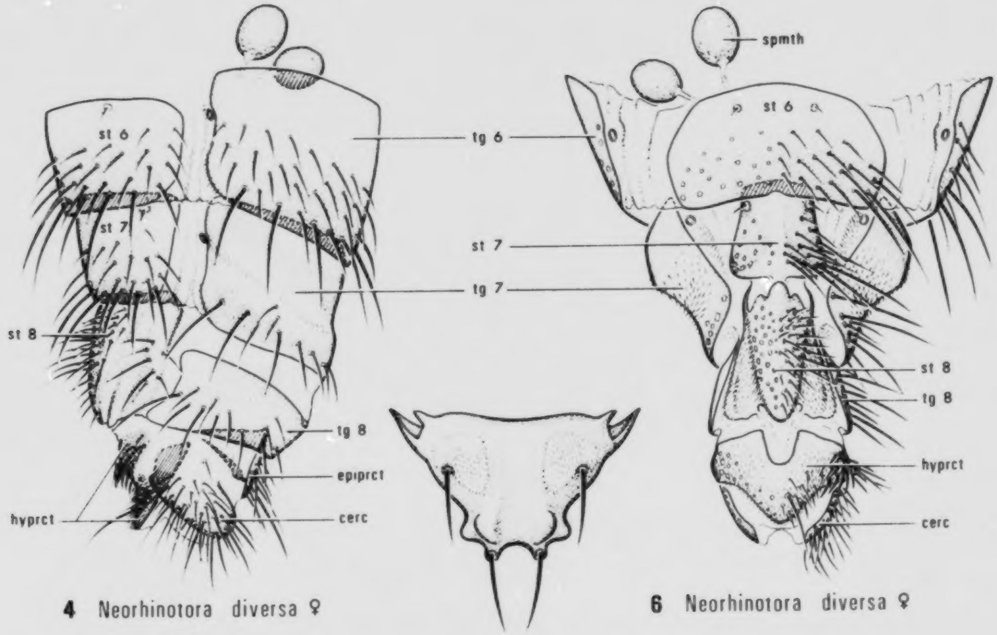
Typical elongate fusiform maggot. Head region completely surrounded by a fringe of slender tentacle-like processes; two pairs of papillae anteriorly, upper ones of which are considered antennae; two pairs of sensory papillae also occurring at each side of atrial opening; another pair of simple processes occurring at posterior margin of this area, with a pair of tooth-like processes between them; heavily ridged transversely serrated paired plates also present above and



2 Neorhinotora diversa ♀

3 Neorhinotora diversa ♂

Figs. 92.2–3. *Neorhinotora diversa* (Giglio-Tos): (2) anterior view of head; (3) wing. Abbreviations: i vt s, inner vertical seta; o vt s, outer vertical seta.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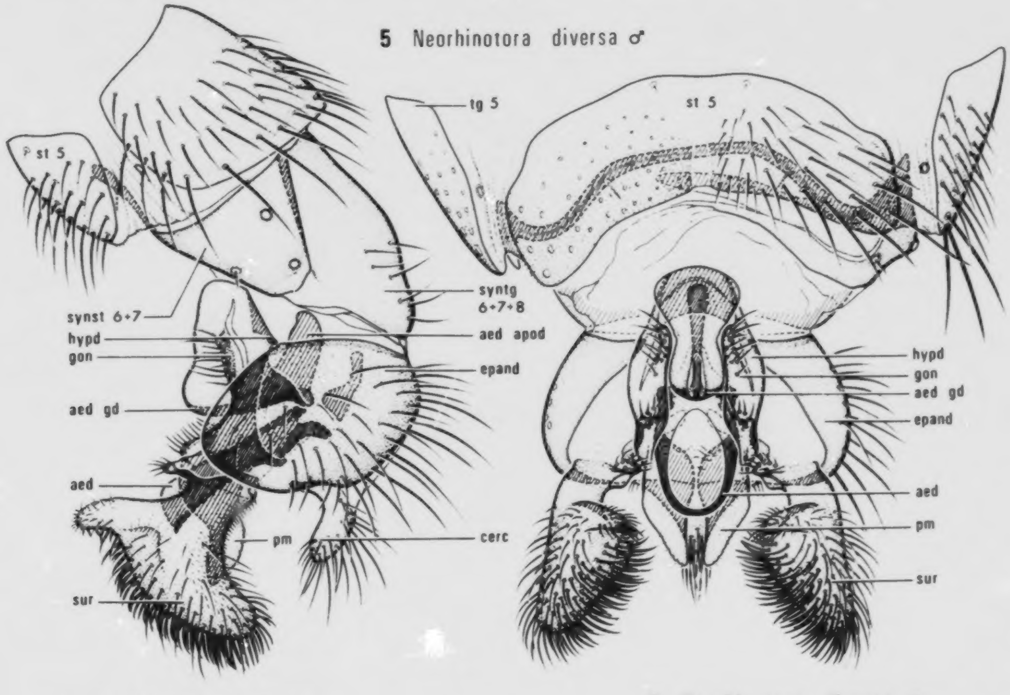
4 Neorhinotora diversa ♀

5 Neorhinotora diversa ♂

6 Neorhinotora diversa ♀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7 Neorhinotora diversa ♂

8 Neorhinotora diversa ♂

Figs. 92.4–8. Terminalia and scutellum of *Neorhinotora diversa* (Giglio-Tos): (4) left lateral and (6) ventral views of female terminalia; (5) scutellum, dorsal view; (7) left lateral and (8) ventral views of male terminalia.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; i vt s, inner vertical seta; o vt s, outer vertical seta; pm, paramere; rc orb s, reclinate orbital seta; spmth, spermatheca; st, sternite; sur, surstylus; synst, synsternite; syntg, syntergite; tg, tergite.

below atrial opening; mandibles simple, with a pair of small rod-like sclerites between and below anterior arms of hypopharyngeal sclerite. Anterior spiracle bearing numerous short branches, all arising from a more or less club-shaped central axis. Posterior spiracles borne on two separate short tubercles at end of a short terminal siphon; each spiracle with three broadly oval openings bordered on inside by short lamellae and partially surrounded by four groups of flattened sometimes branched hydrophobe hairs. Anterior margins of abdominal segments 2–7 bearing well-developed creeping welts armed with numerous short stout slightly hooked spinules.

Biology and behavior. The adults are forest-inhabiting flies, usually found resting on tree trunks or licking sap exuded from wounds or other injuries. They are also attracted to fermenting fruits such as bananas, pineapples, and mangoes. The larvae of the Australian species *Cairnsimyia robusta* were found in tunnels made by cerambycid larvae in *Ficus* (fig tree) (D. K. McAlpine 1968).

Classification and distribution. Only one species of Rhinotoridae is known to occur in the Nearctic region, *Neorhinotora diversa* (Giglio-Tos), from Arizona and New Mexico (Wheeler 1954). The family consists of seven genera: *Rhinotora*, *Rhinotoroides*, *Neorhinotora*, *Anastomyza* Malloch, and *Apophoneura* Malloch (all Neotropical); and *Cairnsimyia* and *Zentula* D. K. McAlpine (Australian-Papuan). D. K. McAlpine (1968, 1985) placed this group of genera as a distinctive tribe, the Rhinotorini, in the family Heleomyzidae. His interpretation is probably phylogenetically sound, but in line with the *Catalog of the Diptera of America North of Mexico*, the group is provisionally treated separately here, as is also done with the Trixoscelididae. The most recent revision of the American genera and species is by Guimarães and Papavero (1966). Papavero (1967) also provided a catalog of all New World species. No fossils are known.

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SPHAEROCERIDAE

93

S. A. MARSHALL AND O. W. RICHARDS

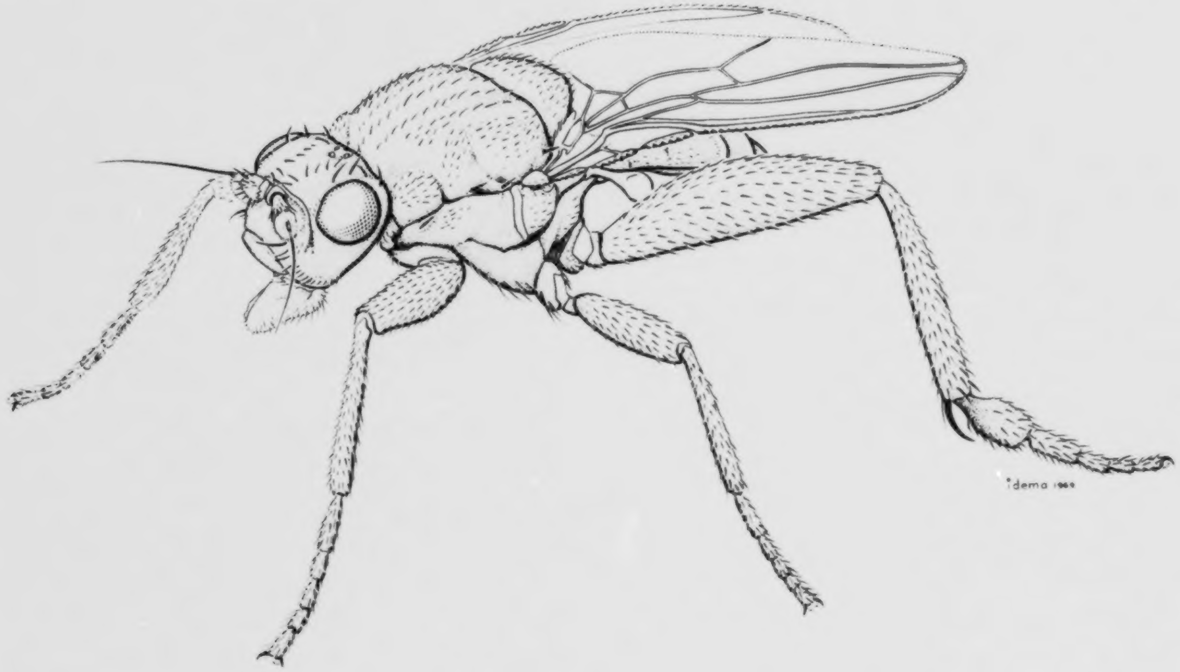


Fig. 93.1. Male of *Sphaerocera curvipes* Latreille.

Small stout-bodied dull-colored flies (Fig. 1), 0.9–5.0 mm long, easily recognized by the short thick first tarsomere of the hindleg. Color usually black or dark brown, sometimes brown or with legs or head yellowish; wings rarely spotted.

Adult. Head: frons broad, slightly narrowed anteriorly (Figs. 10–12, 15–17). Interfrontal bristles usually distinct, arising from narrow, more sclerotized interfrontal plates; typically two proclinate or lateroclinate orbital bristles present, but all bristles very reduced in the subfamily Sphaerocerinae; large inner and outer vertical bristles normally present, the latter situated more anteriorly than usual; paravertical (=inner occipital of Hendel 1928) bristle usually well-developed; outer occipital bristle sometimes strong; postocellar bristles, if present, convergent; vibrissa present; subvibrissal setae forming a distinct row at lower margin of gena, sometimes with anteriormost of these setae nearly as long as vibrissa. Antenna short; first flagellomere rarely a little pointed (Fig. 14), usually rounded (Fig. 13); arista preapical or rarely subapical, usually consisting of three aristomeres. Proboscis relatively short and stout; palpus small.

Thorax: scutum usually setose (Figs. 25, 26), warty in some Sphaerocerinae. Chaetotaxy: typically one or two postpronotal, two notopleural, one presutural supra-alar, one postsutural supra-alar, and one to three postalar bristles present; presutural supra-alar bristle often weak or absent; dorsocentral bristles in one to several pairs; acrostichal bristles usually short; acrostichal setulae in two to ten rows; scutellum bare or with setulae, typically with four marginal bristles, but varying from zero to eight (Figs. 24, 27, 30), or in some Sphaerocerinae with marginal teeth (Fig. 28); anepisternum sometimes with some short setulae (Fig. 26); anepimeron bare; katepisternum with zero (Fig. 26) to three bristles.

Wing (Figs. 2–9) moderately broad to moderately narrow, or reduced or even absent. When wing not reduced, alula well-developed; C with costagial, humeral, and subcostal breaks; C ending at M_{1+2} or at R_{4+5}, or between them; Sc incomplete, fading out just beyond crossvein h; cells bm and dm clearly separated (Figs. 2, 3) or confluent (Figs. 4–9); cell cup closed or open, with A_1 never reaching margin.

Mid tibia, and more rarely hind tibia, often with bristles (Figs. 18–21). Femora, especially hind femur, somewhat stout. Hind tarsus with first tarsomere distinctly swollen, i.e. short and wide, and with second tarsomere somewhat widened and usually longer (Figs. 22, 23).

Abdomen: female usually with seven pairs of spiracles in membrane near ventral margins of tergites (Figs. 38, 39). Male with six pairs of functional spiracles; seventh spiracle on left side sometimes present; sixth and seventh spiracles, when present, on left side enclosed in synsternite 6 + 7 (Fig. 31).

Male abdomen asymmetric behind segment 5; sternite 5 often modified as part of genital pouch. Tergites 6, 7, and 8 greatly reduced or absent; sternites 6 and 7 contiguous or fused and broader on left side, extending ventrally along posterior margin of sternite 5 and contiguous dorsally with sternite 8. Sternite 8 sometimes (Limosininae) fused with tergite 9 (epandrium), and together usually forming a large saddle-shaped sclerite (Fig. 33); sometimes (most Limosininae) fused with the hypandrial arms (Fig. 33); epandrium always bearing large, discrete surstyli. Surstylus sometimes bilobate (Figs. 31, 33), and sometimes trilobate (Fig. 32); inner basal corners of surstyli often connected by a transverse sternite 10. Cercus variably developed, sometimes indistinct, sometimes larger than surstylus and bearing stout spines. Aedeagal apodeme rod-like, mostly free from hypandrium; basiphallus variable, usually more heavily sclerotized than the distiphallus, often with either an epiphallus or an additional process termed a pre-epiphallus, or both; paramere well-developed, usually simple but sometimes complex, asymmetric or setose; gonopod usually, if not always, indistinct or absent; ejaculatory apodeme present or absent, small to large.

Abdomen of female ranging from long and telescoping (Fig. 38) to short and stout (Fig. 39); sternites 1 and 2 usually fused; tergites and sternites partially or totally desclerotized in some groups. Tergites 6, 7, and 8 often desclerotized or modified; tergite 8 often subdivided. Sternite 8 often split longitudinally or otherwise modified, often specifically pigmented; gonopore sometimes surrounded by spines or sclerites in addition to sternite 8 and hypoproct; vagina sometimes sclerotized; hypoproct very variable, usually reduced and partly desclerotized; epiproct reduced, fused with cerci or, rarely, large and heavily sclerotized. Cerci usually simple setose lobes but sometimes with apical spines. Three spermathecae present in most Limosininae or two in Sphaerocerinae and Copromyzinae, variable in shape but usually subspherical and often with apex either invaginated or evaginated into a long process.

Larva. Very little known, but those recorded slender, narrowed anteriorly, with groups of ventral spicules on creeping welts. Mandible very little modified, hooked, without additional teeth. Parastomal bars long, thin, fused to tentoropharyngeal sclerite; hypopharyngeal sclerites long, separate or connected by a weakly sclerotized bridge; skeleton mostly blackish; dorsal cornu narrow, black; dorsal bridge lighter and perforated dorsally. Anterior spiracle rosette-like or branched (Figs. 40, 41); branches sometimes short. Posterior spiracles usually on two subcylindrical lobes; each spiracle with three oval or slit-like openings and three or five groups of interspiracular hairs that are sometimes branched (Figs. 42, 43).

Biology and behavior. Although they are sometimes called small dung flies, dung is only one of many habitats occupied by these flies. North American sphaerocerids are commonly associated with all types of organic decay including dung, carrion, fungi, supralittoral seaweed, compost, mammal nests, conifer duff, cave debris, and small deposits of dead vegetation. Certain species oviposit in the dung balls of dung-rolling scarab beetles (*Ceroptera* Macquart and some *Borborillus* Duda). Elsewhere in the world, sphaerocerids are reported from millipede dung (Villeneuve 1916) and ant nests (Richards 1968).

Although sphaerocerids are among the most abundant and ubiquitous of insects, they appear to be of little direct medical or agricultural importance. *Pullimosina heteroneura* (Haliday) is commonly found in food-processing plants and sometimes reaches nuisance levels in mushroom houses (personal observation). Sphaerocerids have been shown to be the primary means by which mushroom houses become contaminated with nematodes (Haglund and Milne 1974). *Poecilosomella angulata* (Thomson) has caused intestinal myiasis in humans (Micks and McKibbon 1956) and Greenberg (1971) listed an impressive array of pathogenic microorganisms associated with sphaerocerids. Fredeen and Taylor (1964) reported a number of species of Limosininae as infesting sewage disposal tanks. *Thoracochaeta johnsoni* (Spuler) has been recently recognized as a pest in Japanese oyster-processing plants (H. Kurahashi, National Institute of Health, Japan; personal communication). Despite these records, the reclusive habits of these flies likely prevent them from playing a major role in disease transmission.

Sphaerocerids could be of indirect importance to agriculture since they are a major component of the dung community. They could speed up decomposition by grazing on the microfauna and probably have an important effect on community structure. An insect community dominated by sphaerocerids is responsible for the rapid on-shore decay of marine algae, thus contributing significantly to nutrient cycling (Marshall 1979).

It is difficult to generalize about the life cycle of sphaerocerids since our fauna includes a parthenogenic species, *Pullimosina pullula* (Zetterstedt), a species with pupal diapause in winter, *Thoracochaeta seticosta* (Spuler), and at least one species, *Spelobia clunipes* (Meigen), common and active as an adult during midwinter in the subnivean space.

Classification and distribution. This family has many species on every continent, although most faunas are poorly known. Even in the Nearctic, with an estimated 350 species, a large proportion of the species are undescribed. It is not even possible to make a reasonable estimate of the number of Neotropical species; the 174 listed by Richards (1967*b*) are probably a small percentage. The diverse Neotropical fauna includes the most primitive-appearing sphaerocerids, such as *Archiborborus* Duda. Higher classification of the world sphaerocerid fauna is still unsettled; however, the Holarctic fauna includes the subfamilies Sphaerocerinae, Copromyzinae, and Limosininae. The latter group differs most from the postulated primitive state and is the largest and most diverse subfamily. The sphaerocerid species of Australia, monographed by Richards (1973), do not include any native Copromyzinae or Sphaerocerinae, and all are probably descended from littoral Limosininae. The Limosininae include several widespread littoral groups such as *Thoracochaeta* Duda.

Roháček (1982–1983) revised the western Palaearctic *Limosina* complex and divided it into a number of genera, many of which are Holarctic. Within these genera are many Holarctic species, some of which are synanthropic and were probably spread by man. A more common pattern within Holarctic genera is that of disjunct Nearctic–Palaearctic sister-group relations between very close sister species (Marshall 1983*c*, 1984; Marshall and Roháček 1982). Sister-group relationships between higher taxa, such as the North American *Nearcticorpus* Roháček & Marshall and the European *Puncticorpus* Duda, have also been noted (Roháček and Marshall 1982).

Most of the American species were described by Spuler (1923, 1924*a*,*b*,*c*, 1925*a*,*b*,*c*) and keys were provided for their identification, but his work is now out of date. Further species have been described by Malloch (1925), Marshall (1982*a*,*b*,*c*, 1983*a*,*b*,*c*, 1984, 1985*a*,*b*,*c*,*d*), Roháček and Marshall (1982, 1986), Marshall and Roháček (1982, 1984), Sabrosky (1949, 1956), Kim (1968, 1972, 1985), Richards (1960, 1963, 1964, 1967*a*), Norrbom and Kim (1984, 1985*a*, *b*), and Deeming (1980).

Key to genera

1. Wing and halter greatly reduced or absent; halter without a knob. Wing, if present, not extending beyond middle of abdominal tergite 3. Mid tibia without a preapical ventral bristle; hind tibia without a ventral apical spur. Eye large .... LIMOSININAE.... ***Aptilotus*** Mik, in part

13 spp., 6 flightless; western and Appalachian; Marshall 1983*c*

Wing apparently functional; halter with knob. If wing greatly reduced, either a preapical ventral bristle present on the mid tibia (*Leptocera* subgenus *Pteremis* Rondani, Fig. 20), hind tibia with an apical spur (*Crumomyia* Macquart, Fig. 22), eye very small, or R_{2+3} forming an angle of over 60° with R_{4+5} (Fig. 8), and head either red or with silver frontal stripes (*Pterogramma* Spuler) 2

2. Cell cu*p* and cell bm closed (Figs. 2, 3); M and sometimes CuA_1 reaching wing margin (Figs. 2, 3). Only two spermathecae present. Katepisternal bristle usually absent 3

Cell cu*p* open to wing margin, CuA_2 absent, and cell bm confluent with cell dm; M or CuA_1 never reaching wing margin, except as a weak fold (Figs. 4, 9). Three spermathecae usually present. Katepisternal bristle always present .... LIMOSININAE....4

3. CuA_1 reaching wing margin (Fig. 2). Bristles of scutum and scutellum reduced to or replaced by short spines, teeth, or warts (Figs. 26, 28). Anepisternum with a patch of short setae (Fig. 26). Arista bare (Figs. 10, 11) .... SPHAEROCERINAE....36

CuA_1 scarcely produced beyond crossvein dm-cu which is separated from wing margin by less than its own length (Fig. 3). Scutum usually bristly and scutellum with marginal hairs or bristles (Fig. 30). Anepisternum without setae. Arista pubescent (Fig. 12) .... COPROMYZINAE....39

4. Disc of scutellum setulose; at least one pair of marginal setulae between apical scutellar bristles (Fig. 27). Mid trochanter with only short bristles .... ***Coproica*** Rondani

7 spp.; widespread; Richards 1960

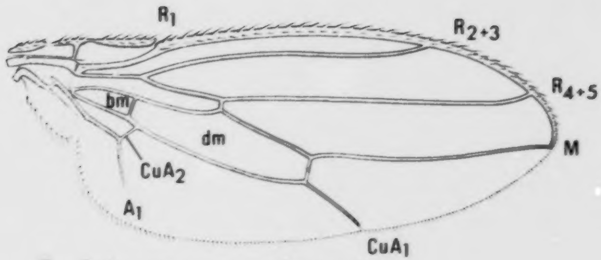
Disc of scutellum usually bare, but if setulose, then mid trochanter with a long curved anteroventral bristle (Fig. 29). Margin of scutellum always bare between apical bristles 5

5. Mid tibia with a long preapical ventral bristle (Fig. 20) or tarsomere 1 of midleg with a long midventral bristle (Fig. 19); mid tibia rarely (subgenus *Pteremis*) with an apicoventral bristle (Fig. 20). Scutellum with four to eight marginal bristles .... ***Leptocera*** Olivier (four subgenera)....6

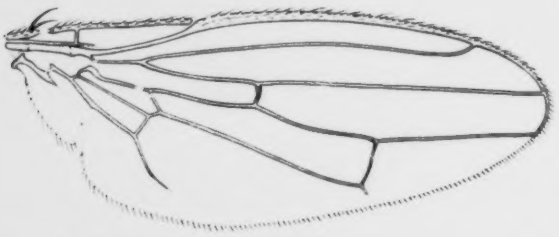
Mid tibia with only minute setae or a row of spinules preapically, almost always with an apicoventral bristle (sometimes absent in male). Scutellum with four marginal bristles, rarely with small additional marginal setulae 9

6. Scutellum with six to eight marginal bristles (Fig. 24). Mid trochanter with a long preapical anterior bristle (Fig. 29) 7

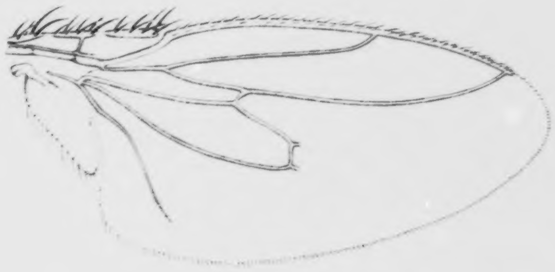
Scutellum with four bristles. Mid trochanter without a long bristle 8



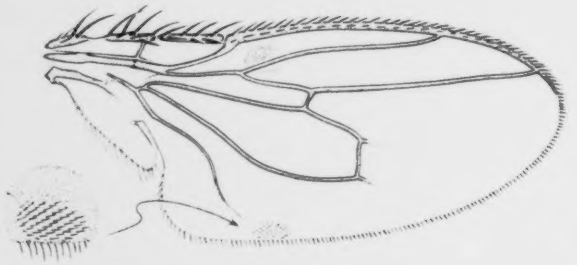
2 Sphaerocera curvipes ♂



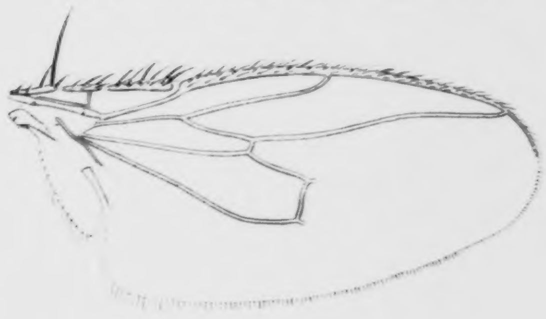
3 Copromyza equina ♀



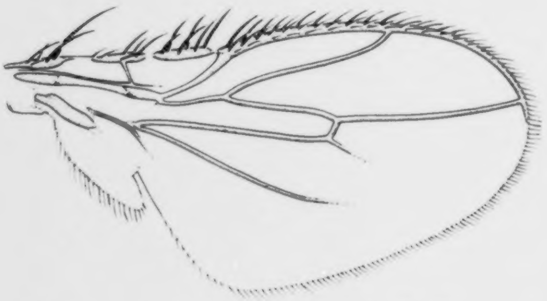
4 Leptocera (Leptocera) fontinalis ♀



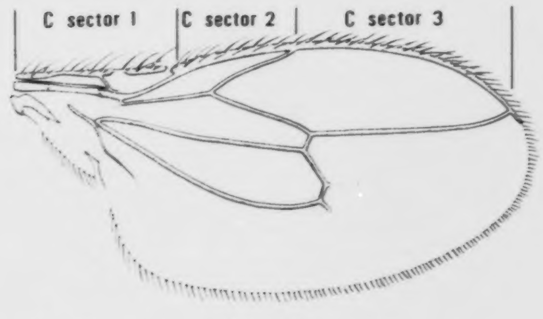
5 Coproica ferruginata ♂



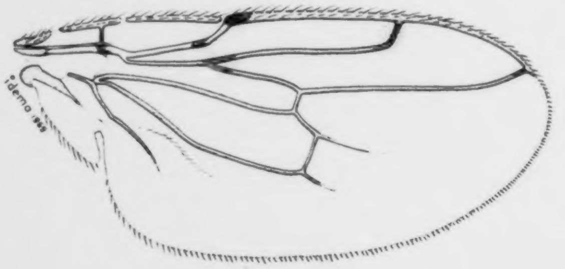
6 Halidayina spinipennis ♀



7 Leptocera (Pteremis) nivalis ♀



8 Pterogramma palliceps ♂



9 Poecilosomella angulata ♂

Figs. 93.2–9. Wings: (2) *Sphaerocera curvipes* Latreille; (3) *Copromyza equina* Fallén; (4) *Leptocera* (*Leptocera*) *fontinalis* (Fallén); (5) *Coproica ferruginata* (Stenhammar); (6) *Halidayina spinipennis* (Haliday); (7) *Leptocera* (*Pteremis*) *nivalis* Haliday; (8) *Pterogramma palliceps* Johnson; and (9) *Poecilosomella angulata* (Thomson).

7. Anterior presutural dorsocentral bristle curving inwards, not oriented like the others (Fig. 25). Facial knob strongly prominent (Fig. 15); head, in side view, projecting in front of eye .... **Leptocera** (**Rachispoda** Lioy)

25 spp.; widespread; Spuler 1924*a* (key, as *Collinella* Duda), Sabrosky 1949 (revision of *lutosa* group)

Anterior presutural dorsocentral bristles small, directed posteriorly. Facial knob small .... **Leptocera** (**Leptocera** Olivier)

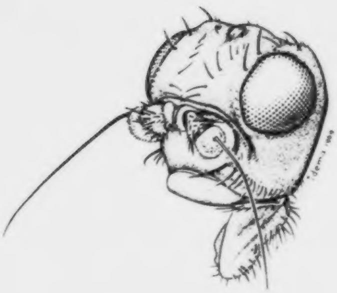
4 spp.; widespread; Spuler 1924*a* (key, as *Paracollinella* Duda)

8. Tarsomere 1 of midleg with a long ventral bristle (Fig. 19); mid tibia lacking apicoventral bristle, but sometimes with preapical ventral bristle .... **Leptocera** (**Opacifrons** Duda)

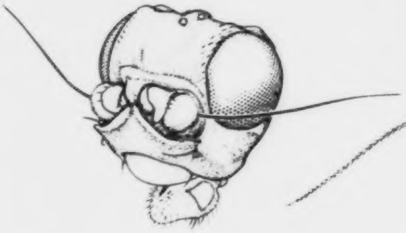
7 spp.; widespread; Spuler 1924*c*

Tarsomere 1 of midleg with only short setae; mid tibia with a preapical ventral bristle and a posteroventral apical one that lies along tarsomere 1 (Fig. 20). Wing sometimes reduced .... **Leptocera** (**Pteremis** Rondani)

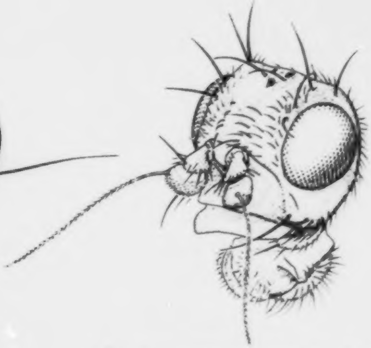
1 sp., *wirthi* Marshall; northern; Marshall 1984



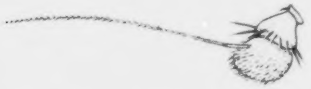
10 Sphaerocera curvipes ♂



11 Mesosphaerocera annulicornis ♂

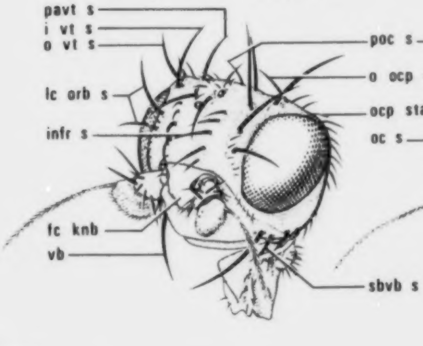


12 Crumomyia annulus ♀

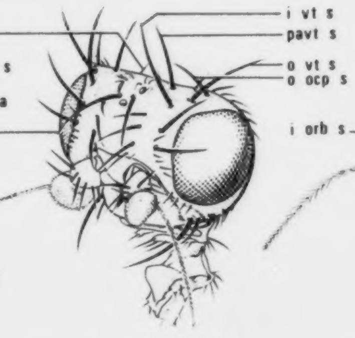


13 Spelobia clunipes ♀

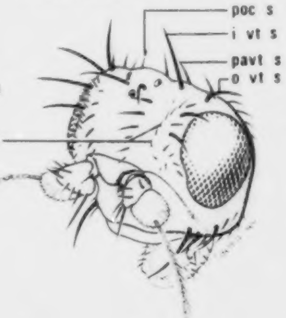
14 Pterogramma palliceps ♂



15 Leptocera (Rachispoda) limosa ♂



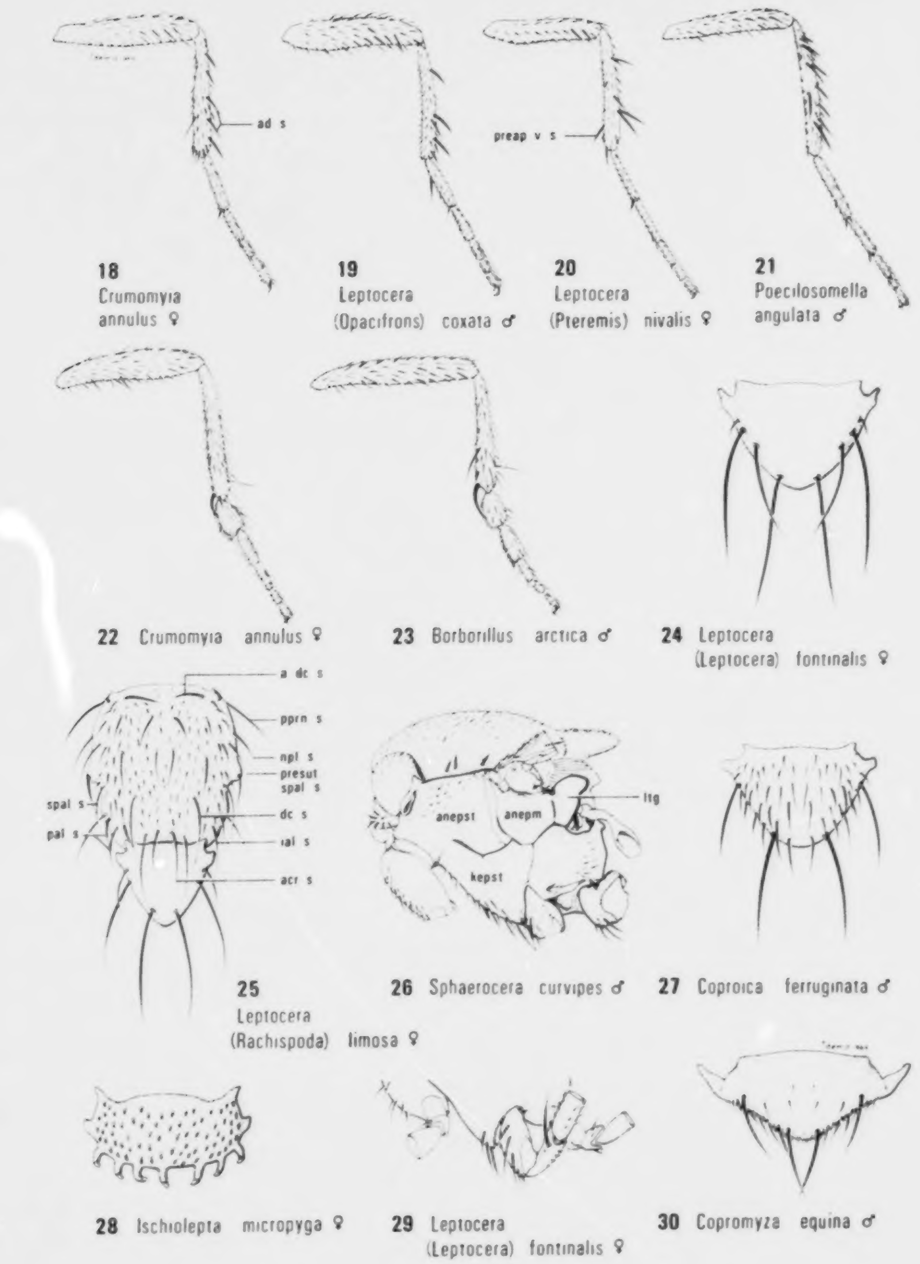
16 Leptocera (Leptocera) fontinalis ♂



17 Halidayina sp. ♂

Figs. 93.10–17. Oblique anterior views of heads and antennae: (10) *Sphaerocera curvipes* Latreille; (11) *Mesosphaerocera annulicornis* (Malloch); (12) *Crumomyia annulus* (Walker); (13) *Spelobia clunipes* (Meigen); (14) *Pterogramma palliceps* Johnson; (15) *Leptocera* (*Rachispoda*) *limosa* (Fallén); (16) *Leptocera* (*Leptocera*) *fontinalis* (Fallén); (17) *Halidayina* sp.

Abbreviations: fc knb, facial knob; infr s, interfrontal seta; i orb s, inner orbital seta; i vt s, inner vertical seta; lc orb s, lateroclinate orbital seta; oc s, ocellar seta; ocp sta, occipital setula; o ocp s, outer occipital seta; o vt s, outer vertical seta; pavt s, paravertical seta; poc s, postocellar seta; sbvb s, subvibrissal seta; vb, vibrissa.



18 Crumomyia annulus ♀

19 Leptocera (Opacifrons) coxata ♂

20 Leptocera (Pteremis) nivalis ♀

21 Poecilosomella angulata ♂

22 Crumomyia annulus ♀

23 Borborillus arctica ♂

24 Leptocera (Leptocera) fontinalis ♀

25 Leptocera (Rachispoda) limosa ♀

26 Sphaerocera curvipes ♂

27 Coproica ferruginata ♂

28 Ischiolepta micropyga ♀

29 Leptocera (Leptocera) fontinalis ♀

30 Copromyza equina ♂

Figs. 93.18–30. Legs and portions of thoraces: (18) anterior views of midlegs of (18) *Crumomyia annulus* (Walker), (19) *Leptocera* (*Opacifrons*) *coxata* (Stenhammar), (20) *Leptocera* (*Pteremis*) *nivalis* Haliday, and (21) *Poecilosomella angulata* (Thomson), lateral views of hindleg of (22) *Crumomyia annulus* and (23) *Borborillus arctica* (Malloch); (24) scutellum of *Leptocera* (*Leptocera*) *fontinalis* (Fallén); thoraces of (25) *Leptocera* (*Rachispoda*) *limosa* (Fallén) in dorsal view and (26) *Sphaerocera curvipes* Latreille in lateral view; scutellum of (27) *Coproica ferruginata* (Stenhammar) and (28) *Ischiolepta micropyga* Duda; (29) basal leg segments of *Leptocera* (*Leptocera*) *fontinalis*; (30) scutellum of *Copromyza equina* Fallén.

Abbreviations: acr s, acrostichal seta; a dc s, anterior dorsocentral seta; ad s, anterodorsal seta; anepm, anepimeron; anepst, anepisternum; dc s, dorsocentral seta; ial s, intra-alar seta; kepst, katepisternum; ltg, laterotergite; npl s, notopleural seta; pal s, postalar seta; pprn s, postpronotal seta; preap v s, preapical ventral seta; presut spal s, presutural supra-alar seta; spal s, supra-alar seta.

9. Crossveins dm-cu and r-m approximated, together forming an almost straight line. R_{2+3} very short; R_{4+5} ending at two-thirds of wing length; C not extending beyond end of R_{4+5}. Very small flies, approximately 1.0 mm, with large postocellar bristles between the paravertical bristles. Hindleg of male of Nearctic species with a long process on tarsomere 4 .... **Bromeloecia** Spuler

3 spp.; eastern, southwestern, and Neotropical; Marshall 1983*a*

Crossveins dm-cu and r-m usually separated by more than the length of crossvein dm-cu; when close together C clearly extending beyond end of R_{4+5}. Size and bristling not as above. Hindleg of male with simple tarsomeres 10

10. Thorax with two or more distinct medioclinate presutural dorsocentral bristles (as in Fig. 25). Species found in decaying seaweed .... **Thoracochaeta** Duda

10 spp.; east and west coasts; Marshall 1982*a*, Marshall and Norrbom 1985 (new species)

Presutural dorsocentral bristles rarely present; if present, minute and never medioclinate 11

11. Scutum with three pairs of postsutural dorsocentral bristles 12

Scutum with one or two pairs of postsutural dorsocentral bristles 13

12. Antenna with scape and pedicel yellow. Mid tibia without a posterodorsal bristle on proximal half. Surstylus simple, in one subquadrate piece .... **Spelobia** (**Bifronsia** Roháček)

1 sp., *bifrons* (Stenhammar); widespread

Antenna with scape and pedicel black. Mid tibia with a proximal posterodorsal bristle. Surstylus separated into anterior and posterior parts (Fig. 32) .... **Kimosina** Roháček

2 descr. and at least 2 undescr. spp.; widespread; Richards 1930 (as *Limosina plumosula* group)

13. Apex of mid tibia with several bristles (as in Fig. 18). Basal half of distiphallus heavily sclerotized. Epiproct of female fused with cerci. Frons of most common species with extra row of setulae (inner orbital setulae) between orbital and interfrontal bristles (Fig. 17). Alula broadly oval; C with one very long costagial bristle (Fig. 6) .... **Halidayina** Duda

3 spp.; 1 widespread sp., others southwestern; Marshall 1982*b*

Apex of mid tibia with one apicoventral bristle or with only small setulae, never with a cluster of bristles. Distiphallus variable. Epiproct of female usually free. Bristling of frons variable. Alula and costagial bristle variable 14

14. Body heavily sclerotized and with punctate appearance. Sternites 2 and 3 of male very large; sternite 4 modified, with one or a pair of posteromedial processes projecting over sternite 5; sternite 5 often reduced or otherwise modified medially. Body length usually over 2.0 mm 15

Body rarely heavily sclerotized, never appearing distinctly punctate. Sternites 2 and 3 of male smaller than the simple sternite 4; sternite 5 usually with posteromedial ornamentation. Body length variable, usually less than 2.0 mm 16

15. Cercus of male large, projecting ventrally, with one or two stout, apical spur-like spines. Tergite 8 of female divided into two or three sclerites; three spermathecae equal in size .... **Apteromyia** Vimmer

2 spp.; eastern; Marshall and Roháček 1982 (females of macropterous *Aptilotus spatulatus* Marshall might also come out here; see couplet 1)

Cercus of male small, not projecting ventrally, without apical spur-like spines. Tergite 8 of known female complete; single spermatheca larger than paired spermathecae .... **Nearcticorpus** Roháček & Marshall

2 spp.; widespread; Marshall and Roháček 1982

16. Costagial bristle long (as in Fig. 6); C ending within two or three times width of vein beyond R_{4+5}. Cercus of female usually spine-like. Sternite 5 of male usually with two dark bare posteromedial lobes (Fig. 37) .... **Rudolfia** Roháček, in part

9 spp.; widespread, mostly southern; Marshall 1982*c*

Costagial bristle usually short, but if long, C extending beyond R_{4+5} by more than length of crossvein dm-cu. Female cercus and sternite 5 of male as above (*Rudolfia*) or differing 17

17. R_{2+3} very short, very close to C, and almost fused with it on distal half; C ending at R_{4+5} .... **Rudolfia** Roháček, in part

see couplet 16

R_{2+3} not as above; if R_{2+3} short, then C extending beyond R_{4+5} 18

18. Male cercus relatively large, larger than surstylus. Female cercus ending in a large curved blunt spine .... ***Rudolfia*** Roháček, in part

see couplet 16

Male cercus smaller than surstylus. Female cercus never ending in a large spine 19

19. Frons with an extra row of bristles or setae, namely the inner orbital bristles, between the orbital and interfrontal bristles (as in Fig. 17); if only one bristle in this position, then costagial bristle long 20

Frons with, at most, a single row of orbital setulae between the orbital and interfrontal bristles (as in Fig. 16) 23

20. Size small; length 0.6–1.5 mm. Inner orbital bristles large. R_{4+5} often strongly curved forward to C and C always extending far beyond apex of R_{4+5} 21

Body length over 2.0 mm. Inner orbital bristles small. R_{4+5} and C ending near tip of wing. Eye less than half as high as gena; antennae close together; face deeply concave and carinate .... ***Ceroptera*** Macquart

1 sp., *sivinskii* Marshall; southeastern U.S.A.; Marshall 1983*b*

21. Alula broadly oval. Inner orbital bristles medioclinate. Hind tibia with more than one dorsal bristle. Sternite 5 of male with two lobes and patches of flat setae .... ***Elachisoma*** Rondani

3 spp.; widespread; Marshall 1982*c*

Alula narrow, pointed. Inner orbital bristles lateroclinate; if only one inner orbital, then costagial bristle long. Hind tibia with, at most, a single dorsal bristle 22

22. Sternite 5 of male with a large posteromedial patch of dark scale-like bristles. Female abdomen narrow, telescoping .... ***Minilimosina zeda*** Marshall

see couplet 35

Sternite 5 of male simple. Female abdomen short .... ***Trachyopella*** Duda

10 spp.; widespread; Roháček and Marshall 1986

23. Apex of R_{2+3} sharply bent forward to C; wing spotted or maculated (Fig 9). Legs with white bands in Nearctic species (Fig. 21) .... ***Poecilosomella*** Duda

1 sp., *angulata* (Thomson); southern U.S.A., Neotropics

Apex of R_{2+3} not sharply bent forward; wing sometimes spotted. Legs never with white bands 24

24. Hind tibia with a long preapical dorsal bristle. Scutellum with only four marginal bristles. Female abdomen narrow, telescoping 25

Hind tibia usually without a preapical dorsal bristle; if present, then female abdomen short and scutellum with a small pair of basal marginal bristles in addition to the usual four marginal bristles, as in *Spelobia maculipennis* (Spuler) 26

25. First flagellomere pointed. One pair of dorsocentral bristles. Two spermathecae. Sternite 5 of male simple; paramere bilobed .... **undescribed genus**

5 spp.; eastern and southern

First flagellomere rounded. Two pairs of dorsocentral bristles. Sternite 5 of male with comb-like posteromedial patches of flat bristles; paramere simple ..... ***Xenolimosina*** Roháček

3 spp.; eastern; Marshall 1985*a*

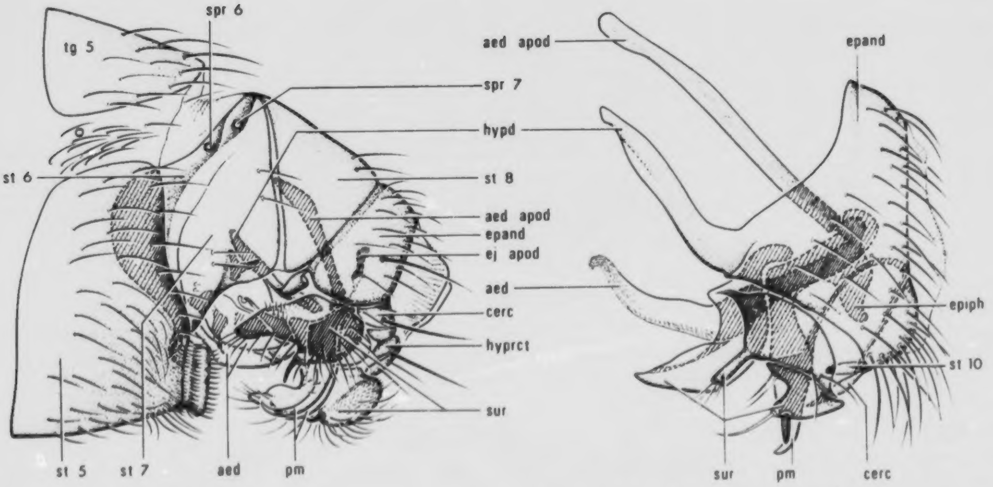
26. R_{2+3} short, running directly from R_{4+5} to C; angle formed by bases of R_{4+5} and R_{2+3} large (over 50°, usually about 65°); second costal sector less than one-half as long as third (Fig. 8); wing often maculated. Head often yellow or with silvery interfrontal stripes .... ***Pterogramma*** Spuler

3 spp.; eastern U.S.A., Neotropics; Spuler 1925*b* (key), Deeming 1980 (new species)

R_{2+3} longer than above; angle formed by bases of R_{4+5} and R_{2+3} less than 50°; second costal sector usually more than one-half as long as third; wing usually clear or uniformly infuscated; if maculated, as in *Spelobia maculipennis* (Spuler), then maculations indistinct 27

27. Cell dm not appendiculate, rounded on posterodistal corner; C extending beyond R_{4+5} by four or five times width of vein; R_{4+5} sinuate; alula broad. Surstylus with a distinct comb-like row of stout bristles ventrally or medially. Abdomen of female long, telescoping. Mid tibia with a midventral bristle except in one rare troglophilic species .... ***Terrilimosina*** Roháček

3 spp.; widespread; Richards 1930 (as *Limosina schmitzi* group), Marshall 1985*b*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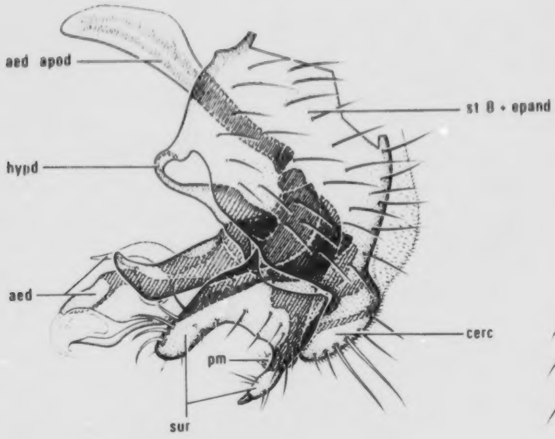
31 Spelobia clunipes ♂

32 Kimosina plumosula ♂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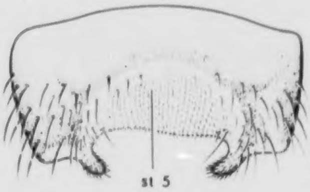
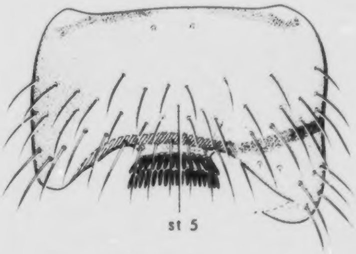
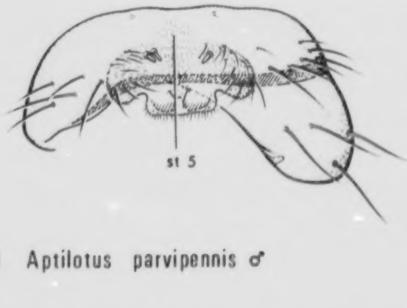
33 Ceroptera sivinskii ♂



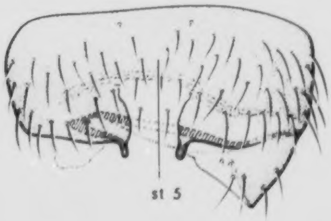
34 Telomerina flavipes ♂



35 Minilimosina sp. ♂



36 Aptilotus parvipennis ♂



37 Rudolfia sp. ♂

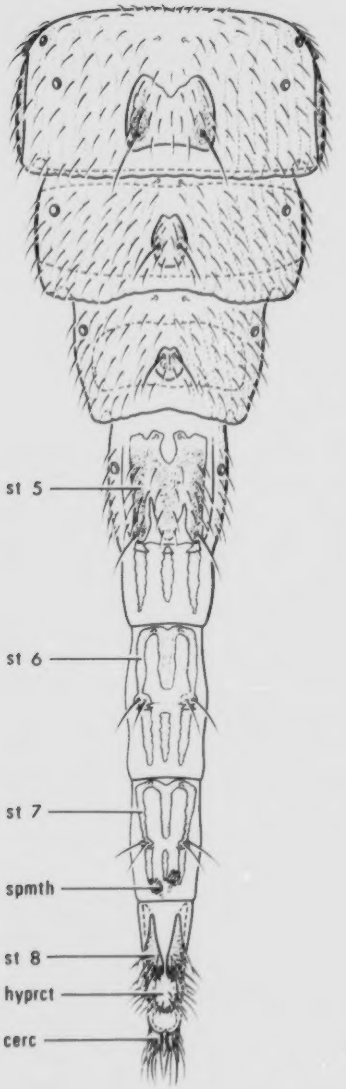
Figs. 93.31–37. Male terminalia: (31) ventrolateral view of entire terminalia of *Spelobia clunipes* (Meigen); lateral views of surstylus of (32) *Kimosina plumosula* (Rondani) and (33) *Ceroptera sivinskii* Marshall; fifth sternites of (34) *Telomerina flavipes* (Meigen), (35) *Minilimosina* sp., (36) *Aptilotus parvipennis* (Spuler), and (37) *Rudolfia* sp.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; hypd, hypandrium; hypd apod, hypandrial apodeme; pm, paramere; spr, spiracle; st, sternite; sur, surstylus; sur lb, surstylar lobe; tg, tergite.

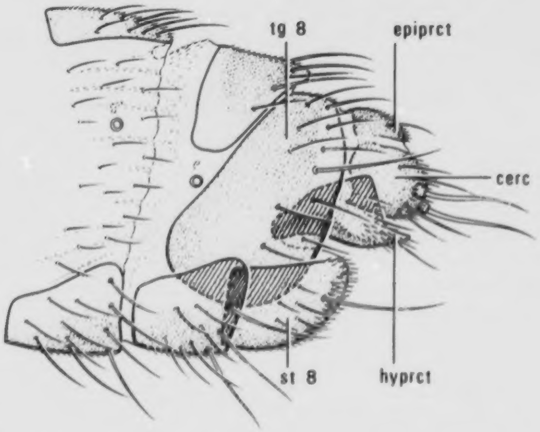
Cell dm usually appendiculate distally, with distal corners angled. Surstylus without a comb. If abdomen of female telescoping and C extending beyond R_{4+5}, then alula narrow and mid tibia with only short setulae in midventral region (*Minilimosina*), otherwise alula and mid tibia variable 28

28. Scutellum with several minute marginal setulae between the basal and apical marginal bristles .... ***Pullimosina*** (***Dahlimosina*** Roháček)

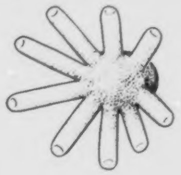
3 spp.; northern; Marshall 1986



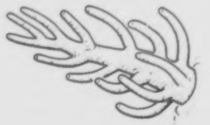
38 Sphaerocera curvipes ♀



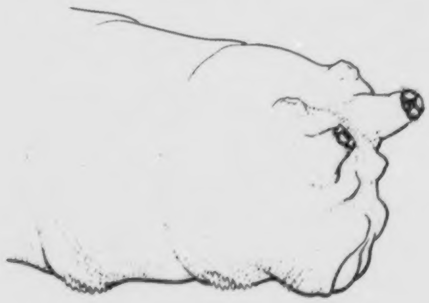
39 Telomerina flavipes ♀



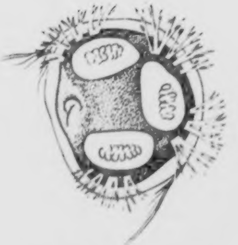
40 Thoracochaeta zosterae



41 Leptocera sp.



42 Leptocera sp.



43 Leptocera sp.

Figs. 93.38–43. Female terminalia and parts of larvae: (38) ventral view of abdomen of *Sphaerocera curvipes* Latreille; (39) lateral view of terminalia of *Telomerina flavipes* (Meigen); anterior larval spiracles of (40) *Thoracochaeta zosterae* (Haliday) and (41) *Leptocera* sp.; (42) terminal segment of larva of *Leptocera* sp.; (43) posterior spiracle of larva of *Leptocera* sp.

Abbreviations: cerc, cercus; epiprct, epiproct; hyprct, hypoproct; spmth, spermatheca; st, sternite; tg, tergite.

Scutellum with at most a single pair of setulae basally, in addition to the usual four marginal bristles 29

29. R_{4+5} ending before wing apex; C extending beyond R_{4+5} by at least as much as the length of crossvein dm-cu. Main part of surstylus subquadrate. Abdomen of female short, with an additional sclerite between sternite 8 and hypoproct. Mid tibia with a midventral bristle in female only. Middle interfrontal bristles cruciate or crossveins dm-cu and r-m separated by less than length of crossvein dm-cu . . . . ***Pullimosina*** (***Pullimosina*** Roháček)

10 spp.; widespread; Richards 1930 (as *Limosina heteroneura* group), Marshall 1986

R_{4+5} ending at or near wing apex; C not extending beyond R_{4+5} by as much as length of crossvein dm-cu. Surstylus not subquadrate, variable. Abdomen of female membranous between sternite 8 and hypoproct. Mid tibia with or without a midventral bristle. Middle interfrontal bristles rarely cruciate and crossveins dm-cu and r-m farther apart than above 30

30. Hind tibia with a long curved preapical ventral spur, as in *Opalimosina mirabilis* (Collin), or scutum with a well-developed bristle midway between and just anterior to intra-alar and posterior dorsocentral bristles. Female with epiproct reduced; male with sharp epiphallus or forked process of sternite 10 projecting between cerci. Body heavily pruinose . . . . ***Opalimosina*** Roháček

3 spp.; widespread; Richards 1930 (as *Limosina appendicula* group), Marshall 1982*c*

Hind tibia with, at most, a minute apical spur and scutum with only setulae between dorsocentral and intra-alar bristles. Female with epiproct well-developed; male never with forked process of sternite 10 and with epiphallus rarely developed. Body polished or pruinose 31

31. Eye small, always less than 2.5 times as high as gena. Surstylus and paramere very long and slender. Sternite 5 of male with posteromedial area concave, membranous, and flanked by setulose lobes (Fig. 34). Abdomen of female short; cercus broader than long (Fig. 39); each spermatheca normally with an unusually long apical projection . . . . ***Telomerina*** Roháček

8 spp.; widespread; Richards 1930 (as *Limosina minutissima* group), Marshall and Roháček 1984

Eyes usually larger than above, but if small, then cercus of female distinctly longer than wide or abdomen long and telescoping. Surstylus and paramere not long and slender. Sternite 5 of male with a single comb-like (Fig. 35) or tab-like (Fig. 36) posteromedial lobe, never concave posteromedially. Each spermatheca with, at most, a small nipple-like apical process 32

32. Head mostly yellow or orange; ocellar triangle, occiput, and antennae brown or black; interfrontal bristles reduced . . . . ***Spelobia*** (***Eulimosina*** Roháček)

1 sp., *ochripes* (Meigen); widespread

Head mostly brown or black; interfrontal bristles variable 33

33. One dorsocentral bristle present, R_{4+5} strongly curved forward to C, and mid tibia with a midventral bristle. Epandrium with stout spine-like bristles . . . . . ***Spinilimosina*** Roháček

1 sp., *brevicostata* (Duda); Florida

More than one dorsocentral bristle present, or R_{4+5} straight and mid tibia without a midventral bristle. Epandrium with slender bristles only, the posterodorsal pair often very long (Fig. 31) 34

34. Mid tibia with a midventral bristle and an apicoventral bristle in both sexes. C ending at R_{4+5}. Two pairs of postsutural dorsocentral bristles present . . . . ***Spelobia*** (***Spelobia*** Spuler)

42 spp.; widespread; Richards 1930 (as *Limosina crassimana* group), Marshall 1985*c*

Mid tibia without a midventral bristle in either sex, with only an apicoventral bristle in female, and with either an apicoventral bristle or a distal row of spinules in male. C usually extending beyond R_{4+5}. One pair of distinct postsutural dorsocentral bristles present; anterior pair of these bristles small or absent 35

35. Sternite 5 of male with a translucent tab-like posteromedial lobe (Fig. 36). Surstylus usually with large inner and outer lobes; if unilobate, then middle interfrontal bristles strongly cruciate. Cercus of female very short, except in *A. spatulatus* Marshall; abdomen short and broad. C usually extending beyond R_{4+5} by less than four times width of vein . . . . ***Aptilotus*** Mik, in part

see couplet 1 (small females of *Apteromyia* and *Nearcticorpus* might also come out here; see couplet 15)

Sternite 5 of male usually with comb-like posteromedial lobe that sometimes includes a median spine, although lacking a comb-like lobe and having the posteromedial part of sternite 5 deflexed in two species. Surstylus variable, but never with large inner and outer lobes; middle interfrontal bristles never strongly cruciate. Cercus of female long; abdomen narrow, telescoping. C usually extending beyond R_{4+5} by more than four times width of vein .... ***Minilimosina*** Roháček

24 spp.; widespread; Richards 1930 (as *Limosina fungicola* group), Marshall 1985*b* (includes subgenera *Minilimosina* Roháček, *Allolimosina* Roháček, *Svarciella* Roháček, and *Amputella* Marshall)

36. Scutellum with, at most, one basal marginal tooth on each side (Fig. 30). Scutum with rows of minute setulae (Fig. 1). Abdominal sternites nearly always more or less reduced, especially in female. Face without a central elevation bounding lower margin of antennal grooves. Hind tibia (Fig. 1) with or without a strong curved apicoventral bristle 37

Scutellum with six or more denticles along posterior margin (Fig. 28). Scutum with rows of warts and wide bare spaces between some rows. Abdominal sternites broad. Face with central elevation that forms a sharp lower boundary to antennal grooves (as in Fig. 11). Hind tibia with a strong, curved apicoventral bristle (as in Figs. 22, 23) .... ***Ischiolepta*** Lioy

5 or more spp.; widespread; Malloch 1925 (key, *Sphaerocera* in part), Richards 1965 (species list)

37. Face not elevated below and antennal grooves not sharply defined (Fig. 10). Abdomen without pale dorsal spots. Hind tibia with (Fig. 1) or without a strong curved apicoventral spur .... ***Sphaerocera*** Latreille

2 spp.; widespread; Kim 1968

Face elevated below so that antennal grooves are defined below by a sharp keel (as in Fig. 11). Abdomen usually with two pale dorsal spots that are large. Hind tibia with a very small apicoventral spur 38

38. Pale dorsal abdominal spots, called membranous intersegmental areas, large. Midline of tergite 3 medially shorter than membranous intersegmental area anterior to it .... ***Parasphaerocera*** Spuler

4 spp.; southern and eastern; Kim 1972

Dorsal membranous intersegmental areas small, although pale surface pruinescence often makes them look large. Midline of tergite 3 much longer than the membranous intersegmental area anterior to it .... ***Mesosphaerocera*** Kim

1 sp., *annulicornis* (Malloch); eastern

39. Genal bristle about one-half to three-fifths length of vibrissa. Head densely setose behind eyes, with postocular setae in numerous irregular rows. Mid tibia with four to five anterodorsal bristles (Fig. 18). Wing crossveins often banded .... ***Crumomyia*** Macquart (including *Fungobia* Lioy)

9 spp.; widespread, mostly northern; Norrbom and Kim 1985*a*

Genal bristle less than one-half length of vibrissa. Head with a single row of postocular bristles. Mid tibia with zero to two anterior and zero to two dorsal bristles. Crossveins not banded unless longitudinal veins also darkened 40

40. Scutellum with four long marginal bristles only. Hind tibia with an anteroventral bristle below middle (Fig. 23). Frons entirely reddish brown to blackish .... ***Borborillus*** Duda

6 spp.; widespread; Spuler 1925*a*, Steyskal 1971

Scutellum with at least six marginal setae, although some may be minute. Hind tibia with only weak anteroventral setae. Frons yellow or orange anteriorly 41

41. Hind tibia with a strong apicoventral bristle. Scutellum with four long and two to many tiny marginal setae. Frons completely pruinose .... ***Copromyza*** Fallén

3 spp.; widespread; Spuler 1925*a*, Norrbom and Kim 1985*b*

Hind tibia without a strong apicoventral bristle. Scutellum with 8–10 short stout marginal setae. Frons with ocellar triangle mostly bare .... ***Lotophila*** Lioy

1 sp., *atra* (Meigen); widespread (as *Olinea* Richards); Norrbom and Kim 1984

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CURTONOTIDAE

94

J. F. McAlpine

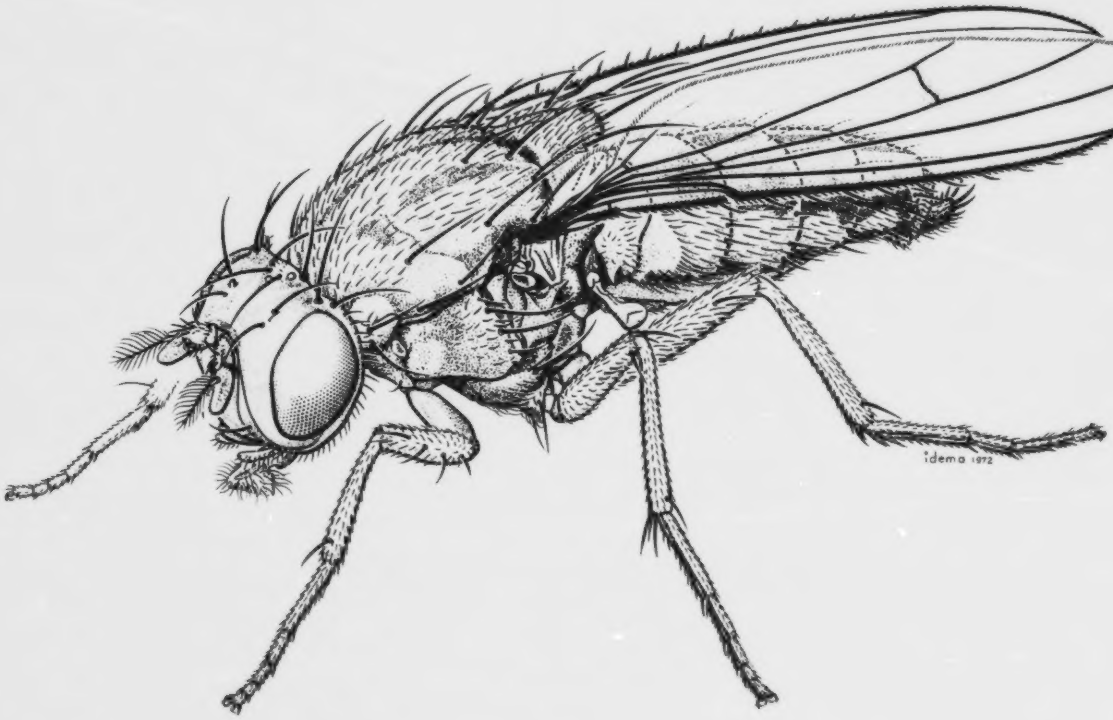


Fig. 94.1. Adult female of *Curtonotum helvum* (Loew).

Medium-sized heleomyzid-like flies (Fig. 1), 4–7 mm long, mostly pale brownish in color, with plumose arista, strongly humped thorax, and lightly fumose wings. Only one species, *Curtonotum helvum* (Loew), known in Nearctic region.

Adult. Head: one-and-a-half times as high as long, strongly bristled (Fig. 1), mainly yellowish. Frons broader than high, with sides almost parallel. Orbital plate a rather narrow pruinose stripe proceeding angularly from vertex toward base of antenna; one strong reclinate bristle arising distinctly below level of anterior ocellus, a slightly smaller proclinate bristle arising almost half way between the reclinate one and the ptilinal suture (absent in Old World genus *Axinota* Wulp), and a very tiny reclinate setula arising between these two bristles but nearer to reclinate bristle; inner and outer vertical bristles strong; ocellar bristles subequal to outer vertical bristles, arising half way between anterior and posterior ocellus; postocellar bristles slightly smaller, strongly cruciate; numerous weak pale setulae covering main surface of frons. Lunule small, unexposed. Face gently concave, with a weak central carina; clypeus small; gena almost as wide as length of first flagellomere; vibrissa present, isolated and larger than subvibrissal setulae. Compound eye high oval, bare. Antenna rather short and decumbent; scape extremely small; pedicel bulging forward as in Drosophilidae, with dorsal seam and apical notch distinct, and with bristling normal; first flagellomere about twice as long as wide, with rounded apex; arista long plumose, with 10 or 11 rays dorsally and five or six below, all subequal in length. Mouthparts and palpus well-developed.

Thorax: scutum strongly arched (Fig. 1), with numerous black setulae; scutellum somewhat flattened above, setulose on disc in *Curtonotum helvum*; prescutellum absent; subscutellum large. Chaetotaxy: two or more postpronotal, one presutural supra-alar, two postsutural supra-alar, one postsutural intra-alar, no presutural and two postsutural dorsocentral, one prescutellar acrostichal, and two notopleural bristles present; two pairs of bristles on scutellum; proepisternal bristle weak; proepimeral bristle absent; two posterior bristles and numerous setulae on anepisternum; one strong bristle, one weak one, and numerous setulae on katepisternum; pleural sclerites otherwise bare. Prosternum broad, bare, extending laterally in front of fore coxae, but not or only weakly fused with propleuron.

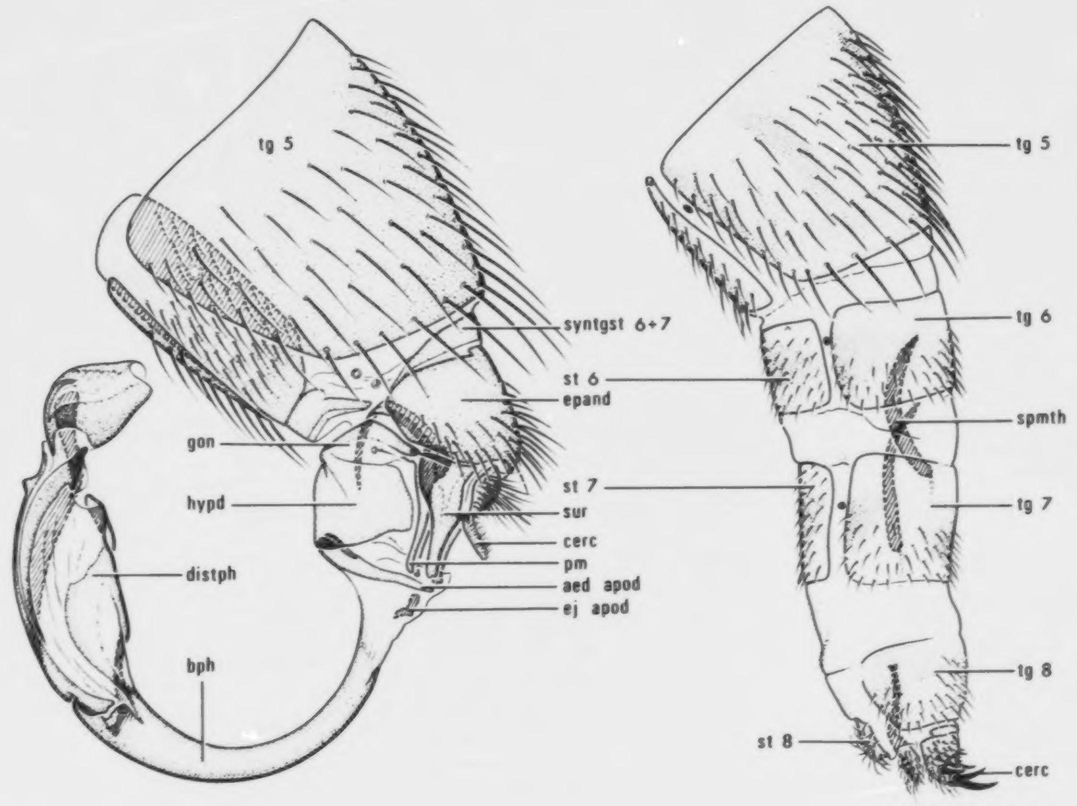
Wing fully twice as long as broad (Fig. 1). C extending to apex of R_{4+5}, strongly spinose between apices of R_1 and R_{2+3}, with both a humeral and a subcostal break; Sc complete; cells dm and bm confluent; crossvein r-m situated before middle of cell dm; last section of CuA_1 slightly shorter than crossvein dm-cu; cell cu*p* present; A_1 weak, not attaining wing margin. Calypteres small, with very short fringe. Halter small, entirely whitish.

Legs rather long and slender (Fig. 1), yellowish. Fore coxa with two bristles; mid coxa with three bristles; hind coxa with one bristle. Fore femur with four posterior bristles and a comb-like row of stubby setulae (ctenidium) on apical third of anteroventral surface; mid femur with six or seven short bristles on anterior surface; hind femur with one short anterodorsal bristle near apex. Each tibia with a strong preapical dorsal bristle; mid tibia also with one weak and two strong ventral bristles at apex.

Abdomen: cylindrical and somewhat tapered to apex (Fig. 1), setulose, and with a row of bristles along posterior margin of segments 2–5. Sternites 1–5 well-developed; sternite 5 somewhat emarginate apically. Spiracles 1–7 present, situated in membrane in both sexes.

Male (Fig. 3) with sternites 6 and 7 present but small and membranized; tergites 6, 7, and 8 mostly membranized and atrophied. Epandrium higher than long in lateral view, setulose along margins. Surstylus long and rather slender, freely articulated with ventral margin of epandrium. Cerci with apices fused and extended into sclerotized median point. Hypandrium a simple U-shaped structure; gonopod in form of low blade, with one anterior setula; paramere long and slender, with slightly expanded apex; aedeagus very large, C-shaped at base, with large asymmetric complicated distiphallus making up apical half; aedeagal apodeme very short, Y-shaped, mostly free from hypandrium, but closely and broadly joined to basiphallus; ejaculatory apodeme unusually small.

Female (Fig. 2) with tubular ovipositor. Tergites and sternites of segments 6–8 free and relatively unmodified. Cerci separate, each with numerous stout upcurved spines in *Cur-*



2 Curtonotum helvum ♂ **3** Curtonotum helvum ♀

Figs. 94.2-3. *Curtonotum helvum* (Loew): left lateral views of (2) male and (3) female terminalia.
Abbreviations: aed apod, aedeagal apodeme; bph, basiphallus; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; sg, segment; spmth, spermatheca; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

tonotum Macquart. Two sclerotized spermathecae present; shape very elongate in *Curtonotum*, short and round in *Axinota*; *Axinota* with a third abnormally shaped spermatheca.

Larva. Immature stages of Nearctic species unknown. The following characters are shown in illustrations (Greathead 1958) of third larval stage of a species identified as *C. cuthbertsoni* Duda, but perhaps not this species (Wirth and Tsacas 1980), from eastern Africa. Posterior end with a ring of short conical fleshy processes. Anterior spiracles with six or seven digits arranged fanwise. Posterior spiracles practically sessile, with three elliptical slits arranged radially in ventral sector of a circular plate-like peritreme; button located dorsal to these slits and surrounded by a ring of thin transparent cuticle. Cephalopharyngeal skeleton with a pair of broad very slightly curved mandibles, each of which is finely serrate on ventral margin. Hypopharyngeal and tentoropharyngeal sclerites very closely associated; dorsal and ventral cornua of tentoropharyngeal sclerite subequal in size, without windows.

Biology and behavior. Greathead (1958) reported that maggots of a *Curtonotum* sp. from eastern Africa feed as scavengers on rotting eggs within the egg pods of the desert locust, *Schistocerca gregaria* (Forskal). Mr. Kevan Barber (personal communication), at Guelph University, reared one adult of *C. helvum* from eggs deposited under laboratory circumstances on egg pods of *Melanoplus* sp. Several species of *Curtonotum* are found in burrows of warthogs and ant bears (Wirth and Tsacas 1980). Cuthbertson (1936) reared *Cyrtona albomacula* Curran from human feces in Rhodesia.

Classification and distribution. Curtonotids have been assigned to various families including the Heleomyzidae, Opomyzidae (as Geomyzidae), Drosophilidae, Diastatidae, and Ephydridae. Enderlein (1914, 1917) placed them as a subfamily (Cyrtonotinae) of the Ephydridae. Hendel (1917, 1928, 1932) treated them as a subfamily (Cyrtonotinae) of the Drosophilidae, which was followed by Malloch (1930). Sturtevant (1921), Curran (1933, 1934), and several other authors (see Sturtevant 1921) also referred them to the Drosophilidae. Duda (1924) and Okada (1960, 1966) placed them in the Diastatidae. Duda (1934) gave them full family status, and this has been followed by most subsequent workers (Hennig 1958, 1971, 1973; Hackman 1960; Delfinado 1969; Griffiths 1972; Tsacas 1974, 1977). They are probably most closely related to the Camillidae and the Drosophilidae.

The family contains about 50 species belonging to three genera, *Curtonotum*, *Axinota*, and *Cyrtona* Séguy, occurring mainly in the tropical and subtropical parts of the Ethiopian, Neotropical, and Oriental regions. One species, *C. helvum*, occurs in the Nearctic region, and a single related species, *C. anus* (Meigen), occurs in the Palaearctic region. No fossils are known.

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DROSOPHILIDAE

95

M. R. Wheeler

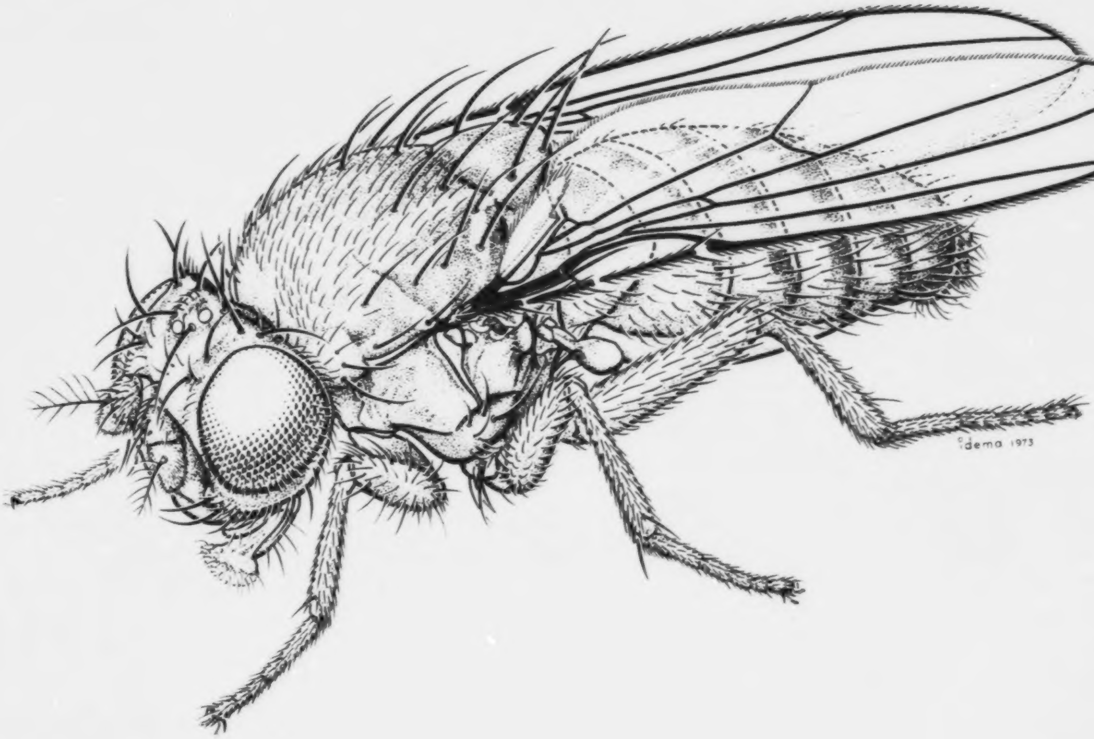


Fig. 95.1. Adult female of *Drosophila melanogaster* Meigen.

Small to moderately large flies (Fig. 1), 1–6 mm long in Nearctic species, usually with bright red eyes when alive. Body pruinose or shiny; color varying from yellow to brown to black, often with stripes or spots on thorax and a pattern of bands or spots on abdomen. Wing hyaline or with distinct darkened areas, sometimes wholly dark. Sexual dimorphism rare, when present involving differences in body color or pattern, body size, wing markings, head shape, or secondary sexual traits such as armature of foreleg.

Adult. Head (Figs. 2–4): eye usually with distinct pile, rarely bare. Three orbital bristles present; usually the anterior one proclinate and the posterior two reclinate, but varying in location on orbital plate; proclinate orbital bristle usually farther from eye margin than either of the reclinate ones. Ocellar bristles large or small; postocellar bristles usually large, sometimes small, always convergent, rarely absent; inner and outer vertical bristles large. Frontal vitta with scattered setulae, sometimes densely so. Face more or less carinate, sometimes flat; one to several well-developed vibrissae present. Arista usually plumose with both dorsal and ventral rays, but sometimes bare, or micropubescent, or with a single dorsal branch, or with a few dorsal branches and none ventral, or some other variation.

Thorax: scutum (Fig. 5) usually with two pairs of postsutural dorsocentral bristles, rarely with just one or with more than two pairs; acrostichal setulae sometimes arranged in two rows, usually in four, six, or eight rows, but with more numerous rows in some genera; prescutellar acrostichal bristles sometimes well-developed; presutural supra-alar bristle only rarely well-developed; postsutural supra-alar bristle present; postalar bristle present; one or two postpronotal bristles present; two notopleural and one to three strong katepisternal bristles present; proepisternal and proepimeral bristles present or absent; anepisternum and anepimeron bare. Legs usually moderately long and slender (Fig. 1); tibiae with apical and preapical dorsal bristles, variable in size. Wing venation usually simple (Figs. 6, 7); C with humeral and subcostal breaks; Sc vestigial apically, but fused with R_1 in *Stegana* Meigen; crossveins r-m and dm-cu always present, but supernumerary crossveins occurring in a few species; A_1 present, or greatly reduced; cells bm and dm sometimes separated by crossvein bm-cu (Fig. 6), sometimes confluent (Fig. 7).

Abdomen: six spiracles usually present in male, seven in female. Male terminalia (Figs. 13, 14) (Hsu 1949; Wheeler and Takada 1963, 1966, 1971; Wheeler 1968; McAlpine

1968) bilaterally symmetric with few exceptions; epandrium (genital arch) with or without lobes or processes on ventral margin; surstylus (clasper) usually with few to many prensisetae or teeth, sometimes subdivided into outer (primary) and inner (secondary, paralobes) lobes; hypandrium U-shaped; gonopods (lateral part of anterior gonopophyses, of Wheeler and Takada 1966) weakly (most *Drosophila* Fallén) to strongly developed (*Paracacoxenus* Hardy); parameres (medial part of anterior gonopophyses of Wheeler and Takada 1966) small to large and heavily sclerotized, sometimes with additional lobes or processes (*Paracacoxenus*); aedeagus short and simple to elongate and very complex; aedeagal apodeme usually elongate and mostly free from hypandrium; ejaculatory apodeme small to relatively large; sternite 10 usually reduced and simple, sometimes with lobes or processes (*Acletotoxenus* von Frauenfeld); cerci (anal plates) short and ventrally directed, sometimes with a coarsely spinose lobe at ventral apex. Female terminalia (Figs. 8–12) with tergite 7 free from sternite 7; sternite 8 frequently divided along midline and modified to form a pair of ovipositor plates (egg guides); hypoproct (subanal plate) simple; epiproct free from bases of cerci in some species, in others indistinguishably fused with cerci; cerci free from each other and from epiproct in some species, in others fused with each other and with epiproct; two spermathecae present, sclerotized, of various sizes and shapes.

Egg. Usually with terminal filaments, from one to about ten depending on the species, but sometimes without filaments.

Larva. Opaque white, with one pair of each of anterior and posterior spiracles. Posterior spiracles usually tan, but black in some species (Figs. 15–19).

Puparium. Tan to brown, with both anterior and posterior spiracles prominent. Anterior spiracles often on elongated stalks (Fig. 20).

Biology and behavior. Larval food habits are varied; most species feed on microorganisms in spoiled fruits, slime fluxes, fungi, rotting cacti, or other decaying organic matter. Some occur in flowers or in flowing sap of tree wounds. Larvae of many species of *Scaptomyza* Hardy are leaf miners; those of *Cladochaeta* Coquillett, as far as known, are ectoparasites of nymphs of Cercopidae; those of *Pseudiastata* Coquillett prey on Pseudococcidae. Numerous species, mainly *Drosophila*, can be maintained in the laboratory on artificial media and are therefore often used in research in genetics, cytology, and insect physiology.

Classification and distribution. The family is large, with about 60 genera containing nearly 3000 described species (Wheeler 1981*a*). Many of the genera are limited to tropical regions of the world. More than half (56%) of the species of the family belong to the large genus *Drosophila*; 40% of approximately 175 known Nearctic species of the family belong to it (Wheeler 1981*b*). It has been divided into 15 so-called subgenera (for Nearctic subgenera see Wheeler 1965), but many of them are weakly differentiated and poorly defined. To date no key has been devised to satisfactorily separate them, and no attempt is made here to segregate them. The same usually applies for the subgenera currently recognized in *Stegana*, *Amiota* Loew, *Leucophenga* Mik, and *Scaptomyza*.

The three Nearctic species assigned to *Gitona* in the following key are not congeneric with the Palaearctic *Gitona* Meigen, including the type-species *G. distigma* Meigen (McAlpine 1968). The correct generic assignment of these three species is still uncertain.

Morphological variation within the family is great; many exceptions to the traits described above occur in certain aberrant species (Wheeler 1981*a*).

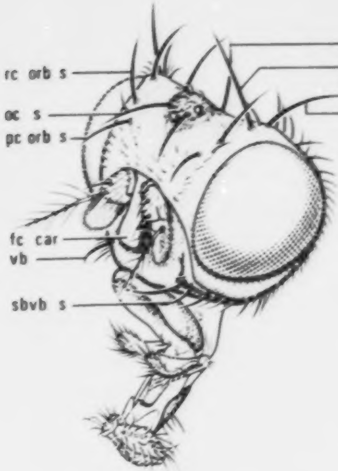
Three fossil species are known. *Drosophila berryi* Cockerell was found in amber from Colombia, South America (Cockerell 1923). The age is uncertain but thought to be Holocene or Pleistocene, or even Tertiary. Wheeler (1963) reported two poorly preserved specimens similar to *Neotanygastrella* Duda in amber from Chiapas, Mexico. Their age is believed to be late Oligocene or early Miocene. *Electrophortica succini* Hennig was described from four specimens from Baltic amber (Hennig 1965) dating back to early Tertiary. These specimens show many resemblances to modern *Amiota*.

Key to genera

1. C deeply incised at subcostal break, and protruding as a thick black lappet (Fig. 7) 2
Subcostal break normal, not forming a protruding lappet (Fig. 6) 4

2. One pair of dorsocentral bristles present; scutellum velvety. Body dark above, pale below .... ***Mycodrosophila*** Oldenberg
3 spp.; widespread; Wheeler and Takada 1963
At least two pairs of dorsocentral bristles present (Fig. 5); scutellum not velvety. Body color various 3

3. Anterior dorsocentral bristles far forward, at or near the transverse suture. Facial carina very large; antennal bases far apart. Acrostichal setulae arranged in two to four rows .... ***Dettopsomyia*** Lamb
1 sp., *nigrovittata* (Malloch); introduced in California
Anterior dorsocentral bristles fairly close to posterior ones. Facial carina small and narrow. Acrostichal setulae arranged in four to eight rows.......... ***Paramycodrosophila*** Duda
2 spp.; southern U.S.A.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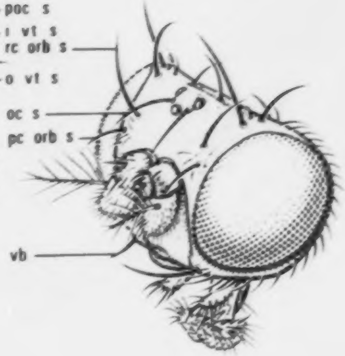
2 Drosophila colorata ♀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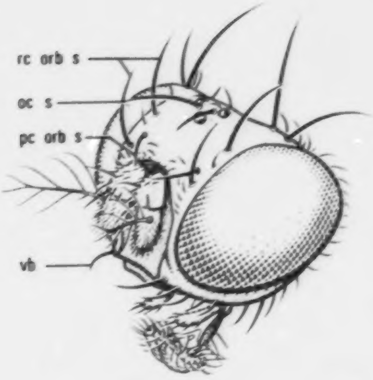
3 Microdrosophila quadrata ♀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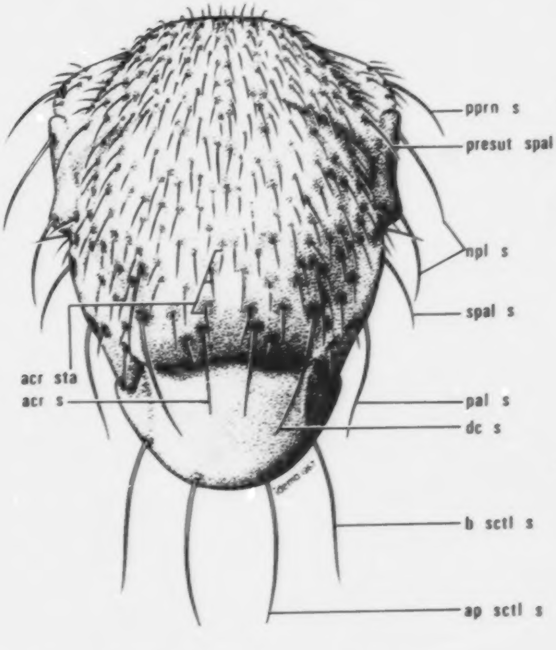
4 Chymomyza amoena ♀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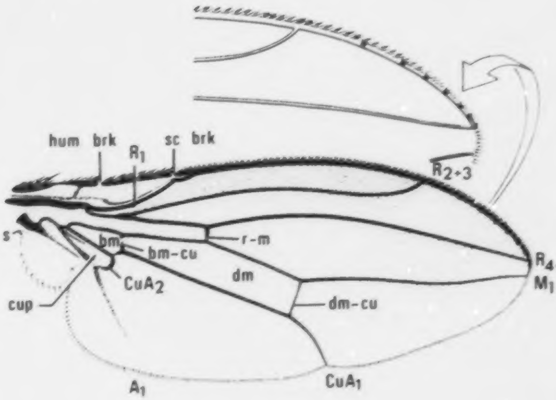
5 Paracacoxenus guttatus ♂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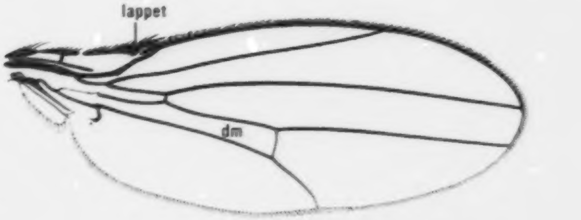
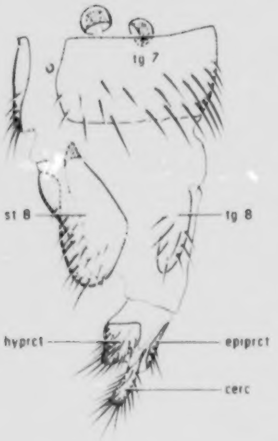
6 Stegana coleoptrata ♂



7 Mycodrosophila claytonae ♂

Figs. 95.2–7. Heads, thorax, and wings: heads of (2) *Drosophila colorata* Walker, (3) *Microdrosophila quadrata* (Sturtevant), and (4) *Chymomyza amoena* (Loew); (5) thorax of *Paracacoxenus guttatus* Hardy & Wheeler, dorsal view; wings of (6) *Stegana coleoptrata* (Scopoli) and (7) *Mycodrosophila claytonae* Wheeler & Takada.

Abbreviations: acr s, acrostichal seta; acr sta, acrostichal setula; ap sctl s, apical scutellar seta; b sctl s, basal scutellar seta; dc s, dorsocentral seta; fc car, facial carina; hum brk, humeral break; i vt s, inner vertical seta; npl s, notopleural seta; oc s, ocellar seta; o vt s, outer vertical seta; pal s, postalar seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; pprn s, postpronotal seta; presut spal s, presutural supra-alar seta; rc orb s, reclinate orbital seta; sbvb s, subvibrissal seta; sc brk, subcostal break; spal s, supra-alar seta; vb, vibrissa.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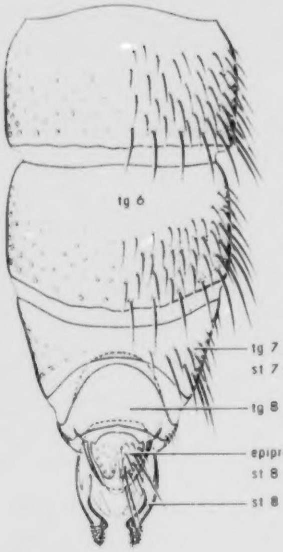
8 Paracacoxenus guttatus ♀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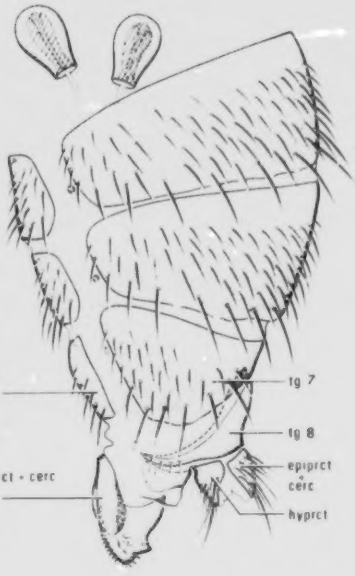
9 Drosophila funebris ♀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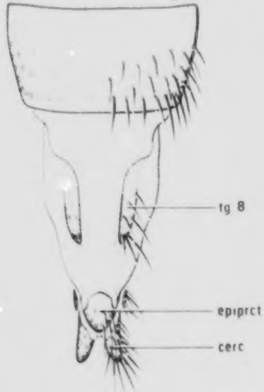
10 Drosophila funebris ♀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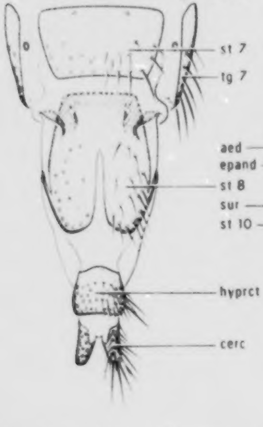
11 Paracacoxenus guttatus ♀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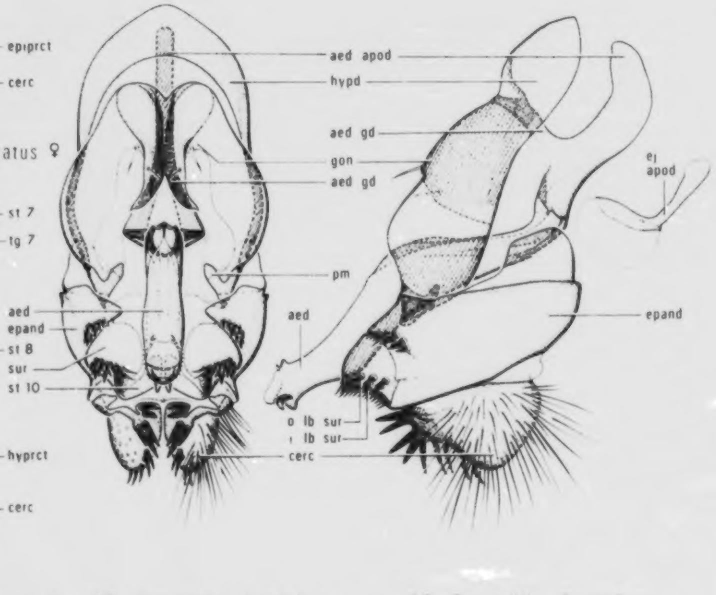
12 Paracacoxenus guttatus ♀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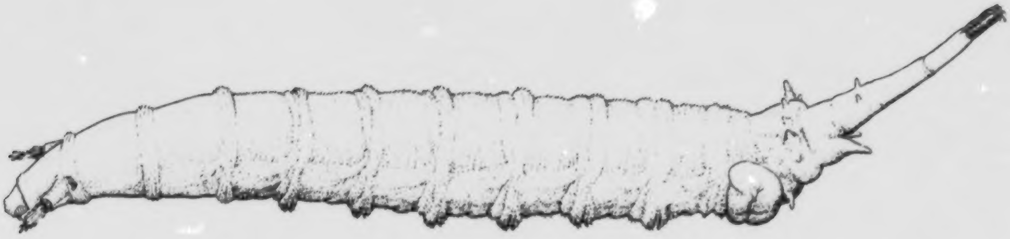
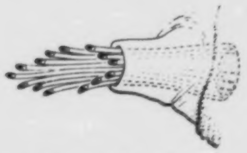
13 Drosophila funebris ♂ 14 Drosophila funebris ♂

Figs. 95.8–14. Terminalia: (8) left lateral, (11) dorsal, and (12) ventral views of female terminalia of *Paracacoxenus guttatus* Hardy & Wheeler; (9) dorsal and (10) ventral views of female terminalia of *Drosophila funebris* (Fabricius); (13) left lateral and (14) ventral views of male terminalia of *D. funebris*.

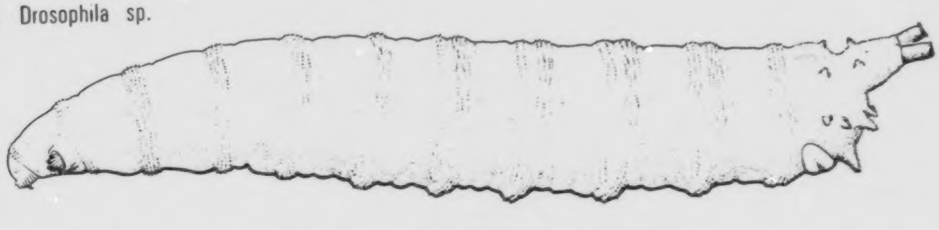
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; i lb sur, inner lobe of surstylus; o lb sur, outer lobe of surstylus; pm, paramere; st, sternite; sur, surstylus; tg, tergite.



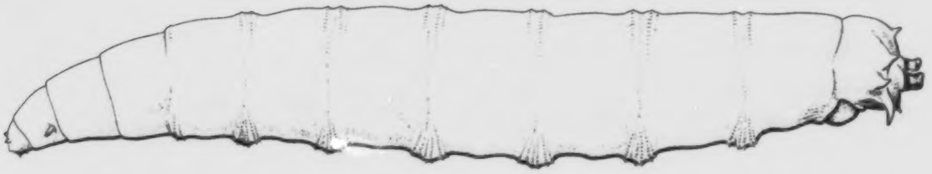
15 Drosophila sp.



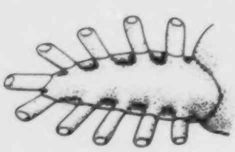
16 Drosophila sp.



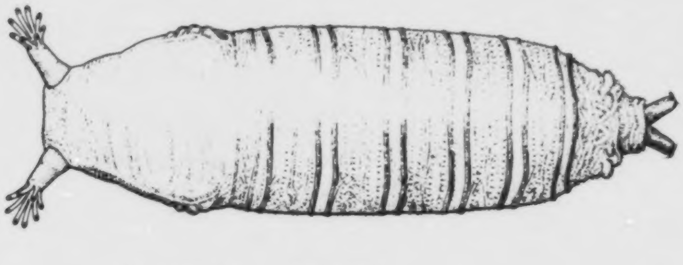
17 Drosophila melanogaster



18 Chymomyza sp.



19 Chymomyza sp.



20 Drosophila melanogaster

Figs. 95.15–20. Larvae and pupa: (15) mature larva of *Drosophila* sp., left lateral view; (16) details of anterior spiracle of larva of *Drosophila* sp.; (17) mature larva of *Drosophila melanogaster* Meigen, left lateral view; (18) mature larva of *Chymomyza* sp., left lateral view; (19) details of anterior spiracle (from puparium) of *Chymomyza* sp., left lateral view; (20) puparium of *Drosophila melanogaster*, dorsal view.

4. Scutum spotted (Fig. 5); spots sometimes partly fused into larger splotches 5

Scutum unicolorous or with longitudinal stripes 9

5. Prescutellar acrostichal bristles weak or absent; basal scutellar bristles convergent; proepisternal bristle absent ....***Drosophila*** Fallén, in part

118 spp.; widespread; Patterson 1943, Wheeler 1981*a* and 1981*b*

Prescutellar acrostichal bristles well-developed (Fig. 5); basal scutellar bristles divergent (Fig. 5); proepisternal bristle present, although sometimes small 6

6. Arista plumose, with numerous dorsal and ventral rays (as in Figs. 2–4). C weak or absent beyond end of R_{4+5} (as in Fig. 7) ....***Leucophenga*** Mik, in part

7 spp.; widespread; Wheeler 1952

Arista bare or micropubescent, sometimes with a few short dorsal rays basally. C clearly continued to end of M_1 (as in Fig. 1) 7

7. Wing with conspicuous dark spots. Facial carina large and prominent (as in Fig. 2). Tibiae with alternating light and dark bands ....***Amiota*** (***Sinophthalmus*** Coquillett)

1 sp., *picta* (Coquillett); southwestern U.S.A.

Wing clear, without spots. Facial carina only weakly developed. Tibiae faintly banded or not at all 8

8. Cells bm and dm separated by a distinct crossvein (as in Fig. 6). Proepisternal bristles absent (Fig. 5). Dark species, with dark legs ....***Paracacoxenus*** Hardy

1 sp., *guttatus* Hardy & Wheeler; northwestern America; McAlpine 1968

Cells bm and dm confluent (as in Fig. 7). Proepisternal bristles well-developed. Brownish species, with pale legs ....***Gitona*** of American authors, not Meigen

3 spp.; southern U.S.A. (*see* Classification and distribution)

9. Arista bare or micropubescent; main stem straight, not bifurcate at apex. Anterior pair of orbital bristles proclinate or strongly convergent ....***Pseudiastata*** Coquillett

2 spp.; southeastern U.S.A.

Arista with one to many dorsal rays and usually with some ventral rays; main stem often bifurcate apically (as in Figs. 2–4). Anterior pair of orbital bristles usually proclinate 10

10. Prescutellar acrostichal bristles present (as in Fig. 5); basal scutellar bristles divergent (as in Fig. 5); proepisternal bristle usually present. Mostly large species, 4–6 mm long 11

Prescutellar acrostichal bristles absent; basal scutellar bristles divergent or convergent; proepisternal bristle absent. Mostly smaller species, up to 3.5 mm long 17

11. Frons very large, thickly covered with small setae. Large species, 5–6 mm or more in length 12

Frons of normal size, with rather sparse scattered setae (Figs. 2–4). Species size usually less than 5 mm 13

12. Frons with numerous small pits in addition to setae. Abdomen mainly black ....***Trachyleucophenga*** Hendel

1 sp., unidentified; southern U.S.A.

Frons without pits. Abdomen tan to brown ....***Rhinoleucophenga*** Hendel

1 sp., *obesa* (Loew); eastern U.S.A., west to Texas and Michigan

13. Wing entirely dark or with some darkly clouded areas (Fig. 6). 14

Wing uniformly hyaline, without darkened areas 16

14. C between apices of R_{2+3} and R_{4+5} with a series of small thorn-like spines along lower margin (Fig. 6). Proepisternal bristle present. Face flat or with a low carina. Species 4–5 mm long 15

C without a series of thorn-like spines. Proepisternal bristle absent. Face flat. Small species, less than 2.5 mm long ....***Cladochaeta*** Coquillett, in part

5 spp.; widespread; Wheeler and Takada 1971

15. Face carinate. C reaching apex of M_1. R_{4+5} and M_1 strongly convergent apically (Fig. 6). Mid tibia with a row of strong posterodorsal bristles ....***Stegana*** Meigen

3 spp.; widespread

Face flat. C weak or absent beyond end of R_{4+5}; R_{4+5} and M_1 converging slightly or not at all. Mid tibia without strong bristles ....***Leucophenga*** Mik, in part

see couplet 6

16. Cells bm and dm separated by a crossvein (as in Fig. 6). Tan to black flies, with milky white markings on face, postpronotal lobes, and areas below wing bases. Species 3–5 mm long .... ***Amiota*** (***Amiota*** Loew)

8 spp.; widespread

Cells bm and dm confluent (as in Fig. 7). Flies without milky white areas on face and thorax. Smaller species, 1.5–3 mm long .... ***Drosophila*** (***Scaptodrosophila*** Duda)

3 spp.; southwestern U.S.A.

17. Apical scutellar bristles divergent (as in Fig. 5); anterior dorsocentral bristles placed far forward, at or near transverse suture. Proclinate orbital bristle arising laterally to strong reclinate orbital bristle (Fig. 3) .... ***Microdrosophila*** Malloch

1 sp., *quadrata* (Sturtevant); eastern Canada and U.S.A. west to Texas

Apical scutellar bristles cruciate; anterior dorsocentral bristles not placed far forward. Proclinate orbital bristle arising medially to reclinate orbital bristles (Figs. 2, 4) 18

18. Postocellar bristles small and inconspicuous; proclinate or inclinate orbital bristle arising posterior to, i.e. above, and about equal in size to anterior reclinate orbital bristle (Fig. 4). Inner margin of fore femur always armed with a row of short teeth .... ***Chymomyza*** Czerny

8 spp.; widespread; Wheeler 1952

Postocellar bristles usually well-developed; proclinate orbital bristle arising anterior to, i.e. below, anterior reclinate orbital bristle and distinctly stronger than it (Fig. 2). Fore femur rarely armed with a row of teeth 19

19. Face flat. Arista with one to five dorsal rays and one or no ventral rays. One strong katepisternal bristle present. Wing usually with darkened areas .... ***Cladochaeta*** Coquillett, in part

see couplet 14

Face carinate, at least on upper half (Fig. 2). Arista with numerous dorsal rays and one to many ventral rays. Usually two or three katepisternal bristles present. Wing clouded or not 20

20. Acrostichal setulae arranged in two or four rows. Arista with only one or two ventral rays. Slender flies, with rather long slender legs .... ***Scaptomyza*** Hardy

22 spp.; widespread; Wheeler and Takada 1966

Acrostichal setulae usually arranged in six or more rows, rarely in four rows. Arista usually with more than two ventral rays (Fig. 2). Body shape various .... ***Drosophila*** Fallén, in part

see couplet 5

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DIASTATIDAE

96

J. F. McALPINE

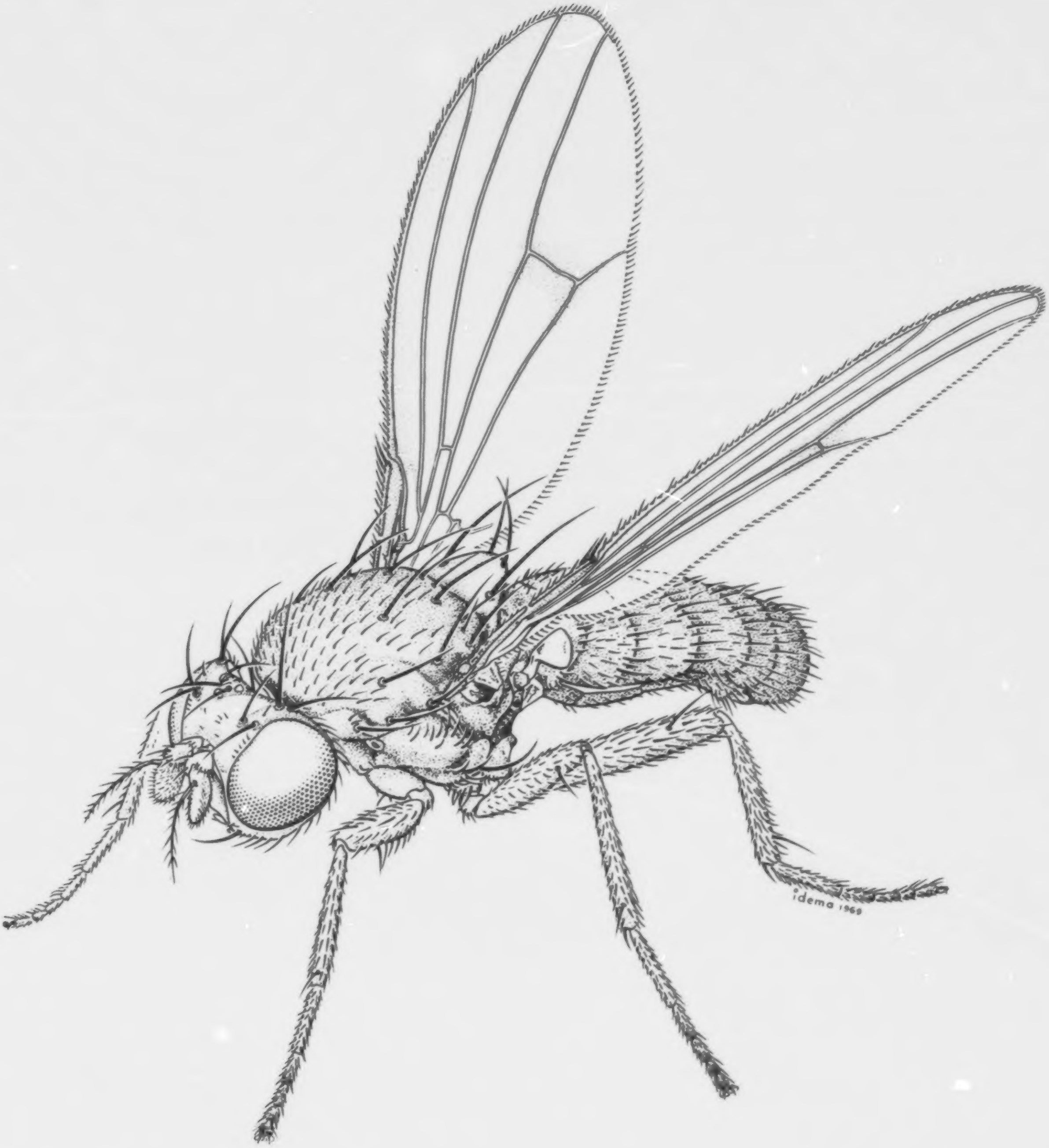


Fig. 96.1. Adult male of *Diastata vagans* Loew.

Small grayish brown drosophilid-like flies (Fig. 1), 2.5–4.0 mm long, usually with patterned wings and weakly spinose C (Fig. 3).

Adult. Head: higher than long, with strong bristles and sparse setulae (Figs. 1, 2). Frons often strongly narrowed from vertex to lunule; orbital plates rather isolated. Two reclinate orbital bristles arising near inner anterior margin of orbital plate; lower one much stronger than upper one in *Diastata* Meigen; upper one stronger than lower one in *Campichoeta* Macquart and in the Palaearctic genus *Euthychaeta* Loew; one strong proclinate orbital bristle arising laterally to reclinate ones; ocellar bristles strong, arising on ocellar tubercle between anterior and posterior ocelli; inner vertical bristles frequently stronger than outer ones; postocellar bristles convergent, about equal in size to outer vertical bristles; frontal vitta very finely and sparsely setulose. Lunule concealed. Face almost flat, without median carina or antennal grooves; gena narrow; cheek usually less than half width of first flagellomere; clypeus linear. Vibrissa strong; five to seven subvibrissal setulae in a single row. Compound eye high oval, bare. Antenna short to moderately long; pedicel swollen dorsally and with weak apical notch and dorsal seam as in Drosophilidae; first flagellomere strongly decumbent, one to three times as wide as pedicel; arista practically bare to moderately long plumose. Mouthparts and palpus normal.

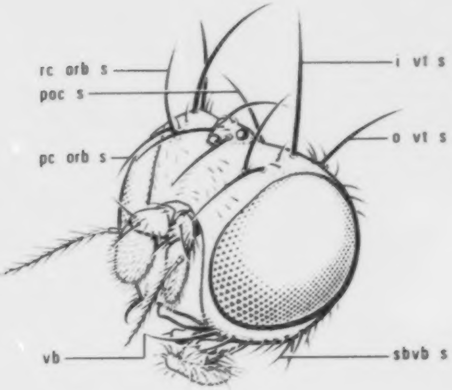
Thorax: dull to subshining (Fig. 1). Scutellum with flattened bare disc; prescutellum absent; subscutellum moderately strong. Prosternum bare, broad anteriorly, but not fused with pleuron. Metasternal area bare. Chaetotaxy: scutum setulose but not densely so, with setulae depressed and arranged in regular rows; one postpronotal and one presutural supra-alar bristle, two postsutural dorsocentral bristles, zero or one postsutural acrostichal bristle, one postsutural supra-alar bristle, two postalar bristles, and two notopleural bristles present; scutellum with two pairs of bristles; proepisternal and proepimeral bristles weak; anepisternum bare or setulose; katepisternum with one strong bristle and one or two weaker bristles, and with numerous setulae; other pleural sclerites bare.

Wing (Fig. 3) rather long and narrow, usually fully twice as long as broad. Anal lobe and alula rather weak to virtually absent. C extending to M_{1+2} but weak between apices of R_{4+5} and M_{1+2}, rather weakly but distinctly spinose, with both humeral break and subcostal breaks present; Sc incomplete; cell bm and cell dm separated by crossvein bm-cu, sometimes weakly so; crossvein r-m far proximal to middle of cell dm; last section of CuA_1 usually about as long as crossvein dm-cu; cell cu*p* complete; A_1 weak, short, not reaching wing margin. Wing membrane usually with brownish spots on subhyaline background or with whitish spots on brownish background.

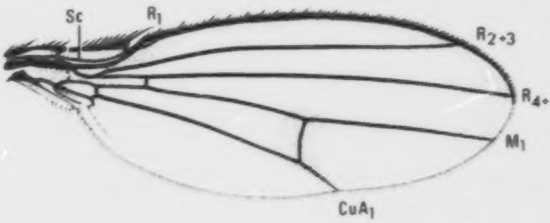
Legs rather elongate and slender (Fig. 1). Fore femur always with a comb of short stout setae (ctenidium) on apical half of anteroventral surface (Fig. 4), also with several to five or six bristles on posterodorsal and posteroventral surfaces; mid femur, especially in male, almost always with a ctenidium on apical half of posteroventral surface (Fig. 5); anterior surface also with series of normal bristles; hind femur with a few bristles near apex on anterior surface. All tibiae with one well-developed preapical dorsal bristle; mid and hind tibiae with one to several apical ventral bristles.

Abdomen: cylindrical with segments 1–5 unmodified in both sexes.

Male with segments 6–8 greatly reduced (Figs. 6, 7), usually with six pairs of spiracles situated in membrane; spiracle 7 when present (*Campichoeta*) very small and probably nonfunctional; sternite 6 shifted into left side; tergite 6 fairly large to almost absent, frequently divided dorsally with a portion on each side of meson; syntergosternite 7+8

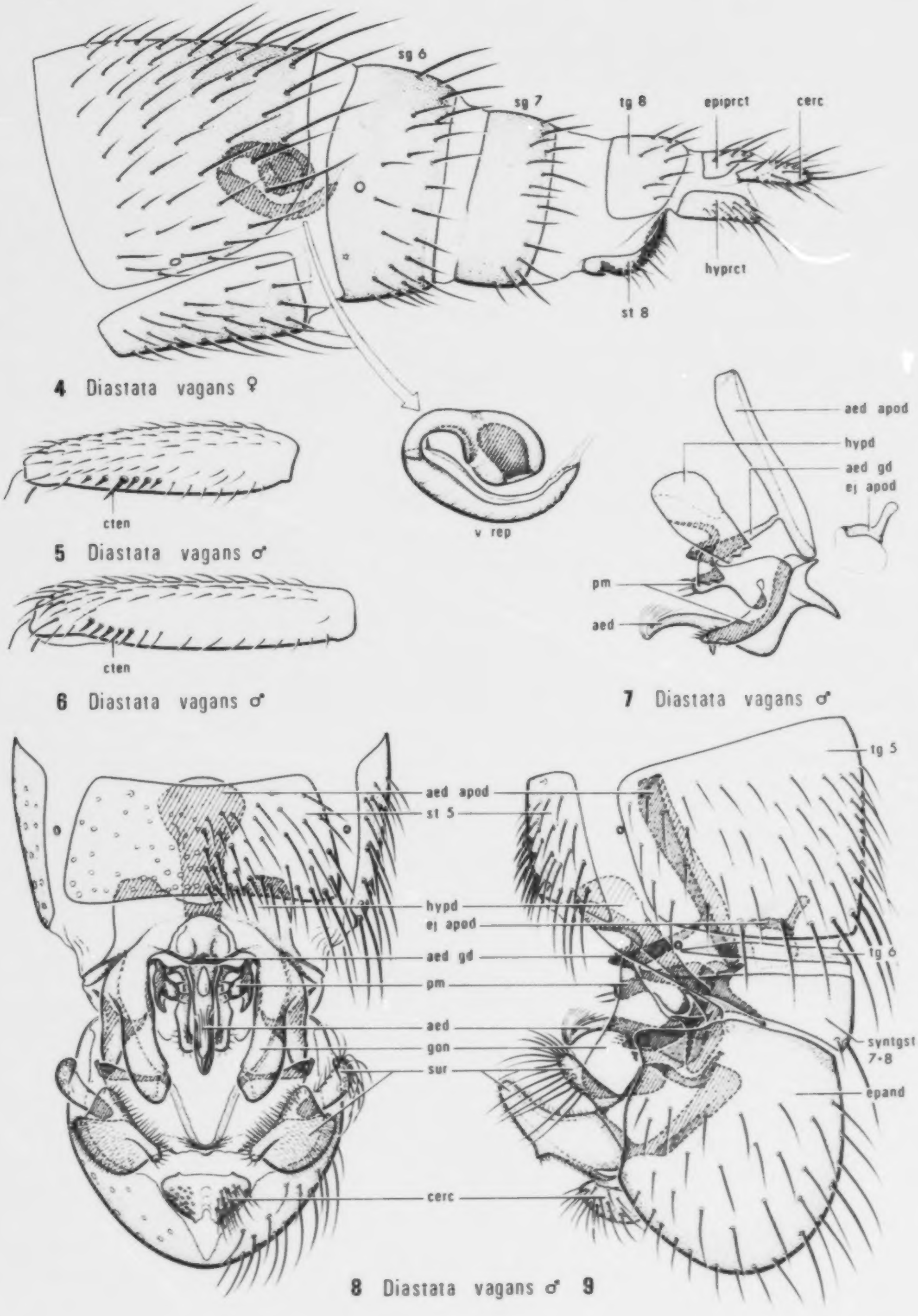


2 Diastata vagans ♀



3 Diastata vagans ♂

Figs. 96.2–3. *Diastata vagans* Loew: (2) head; (3) wing (*continued*).
Abbreviations: i vt s, inner vertical seta; o vt s, outer vertical seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; rc orb s, reclinate orbital seta; sbvb s, subvibrissal seta; vb, vibrissa.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Figs. 96.4–9. *Diastata vagans* Loew (*concluded*): (4) left lateral view of female terminalia, with enlargement of ventral receptacle; (5) right front femur, anterior surface; (6) left mid femur, posterior surface; (7) details of paramere and associated parts of male terminalia; (8) ventral and (9) left lateral views of male terminalia.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; cten, ctenidium; ej apod, ejaculatory apodeme; epiprct, epiproct; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; sg, segment; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; v rep, ventral receptacle.

usually fairly symmetric, in dorsal position, usually setulose; tergite 8 indistinguishable. Epandrium relatively broad in side view; surstylus usually unilobate (*Campichoeta*, *Euthychaeta*) or bilobate (*Diastata*), solidly fused with epandrium or freely articulated, occasionally absent. Cerci short, rather fleshy. Hypandrium heavily sclerotized, U-shaped; gonopod blade-like; paramere closely applied to base of aedeagus; aedeagus rigidly sclerotized, frequently C-shaped in lateral view; aedeagal apodeme rod-like with expanded apex, free from hypandrium.

Female (Fig. 8) with six (*Diastata*, *Euthychaeta*) or seven (*Campichoeta*) pairs of spiracles. Ovipositor tubular, with its segments folding together telescope-like. Segment 6 with tergite and sternite sometimes fused into a continuous ring (*Diastata*); segment 7 sometimes likewise (*Diastata*); sternite 8 and sometimes sternite 7 divided along midline. Cerci free from each other, with numerous setulae and hairs. Two spermathecae present, sclerotized (*Campichoeta*, *Euthychaeta*) or unsclerotized (*Diastata*). Ventral receptacle weakly sclerotized (*Campichoeta*, *Euthychaeta*) or heavily so (*Diastata*) (Fig. 8).

Biology and behavior. Immature stages and biology of Nearctic species are unknown. Hennig (1968) treated a drosophilid-like larva of uncertain origin and identified it as a member of the Diastatidae, possibly *Campichoeta punctum* Meigen, but this identification needs confirmation. Adults frequent low deciduous shrubs along margins of bogs, marshes, and other lush forest-edge habitats. Males of some species of *Diastata* vibrate their wings in otitid-like fashion when sexually excited.

Classification and distribution. The Diastatidae are members of the Ephydroidea. Two apomorphic characters shared by all members of the family and proving the monophyly of the four genera here assigned to it are the well-developed ctenidium on the fore femur (Fig. 4) and the series of fine, evenly spaced spines on C (Fig. 3). Griffiths (1972) separated *Diastata* from *Campichoeta* and *Euthychaeta* (his Campichoetidae) and placed it in the Ephydridae, mainly on the grounds that females of *Diastata* and Ephydridae have a heavily sclerotized ventral receptacle. This arrangement is rejected for several reasons: the ventral receptacle of *Diastata* (Fig. 8) differs in form and position from the type found in the Ephydridae, and resemblances in this respect are not judged to be especially significant (Sturtevant 1942, Sturtevant and Wheeler 1954). Moreover, *Diastata* and all other members of the family differ from all Ephydridae in having convergent postocellar bristles (absent in Ephydridae, but often replaced by pseudopostocellar bristles, i.e. specialized ocellar setulae), cell cup present (absent in Ephydridae), crossvein bm-cu present (absent in Ephydridae), preapical dorsal bristles on all tibiae (absent on mid and hind tibiae in Ephydridae), and abdominal spiracles in the pleural membrane (enclosed in tergites in Ephydridae). These combinations of characters show that Diastatidae and Ephydridae are best treated as separate, mutually exclusive families.

The family occurs mainly in the Holarctic region, with a few species reaching into the bordering Oriental (Nepal) and the Neotropical (Mexico, Brazil) regions; Cogan (1975) recently described three species of *Diastata* from Africa. In all about 22 species belonging to three genera, *Campichoeta*, *Diastata*, and *Euthychaeta*, are described, mostly from Europe and North America. Several undescribed species, especially in the genus *Diastata*, are known. Two fossil species, *Pareuthychaeta electrica* Hennig and *P. minuta* (Meunier) from Baltic amber, are known (Hennig 1965).

Key to genera

1. Katepisternum setulose . . . . ***Diastata*** Meigen
5 spp., plus several more undescribed species; throughout temperate North America
Katepisternum bare . . . . ***Campichoeta*** Macquart
2 spp.; throughout North America; McAlpine 1962

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CAMILLIDAE

97

J. F. McAlpine

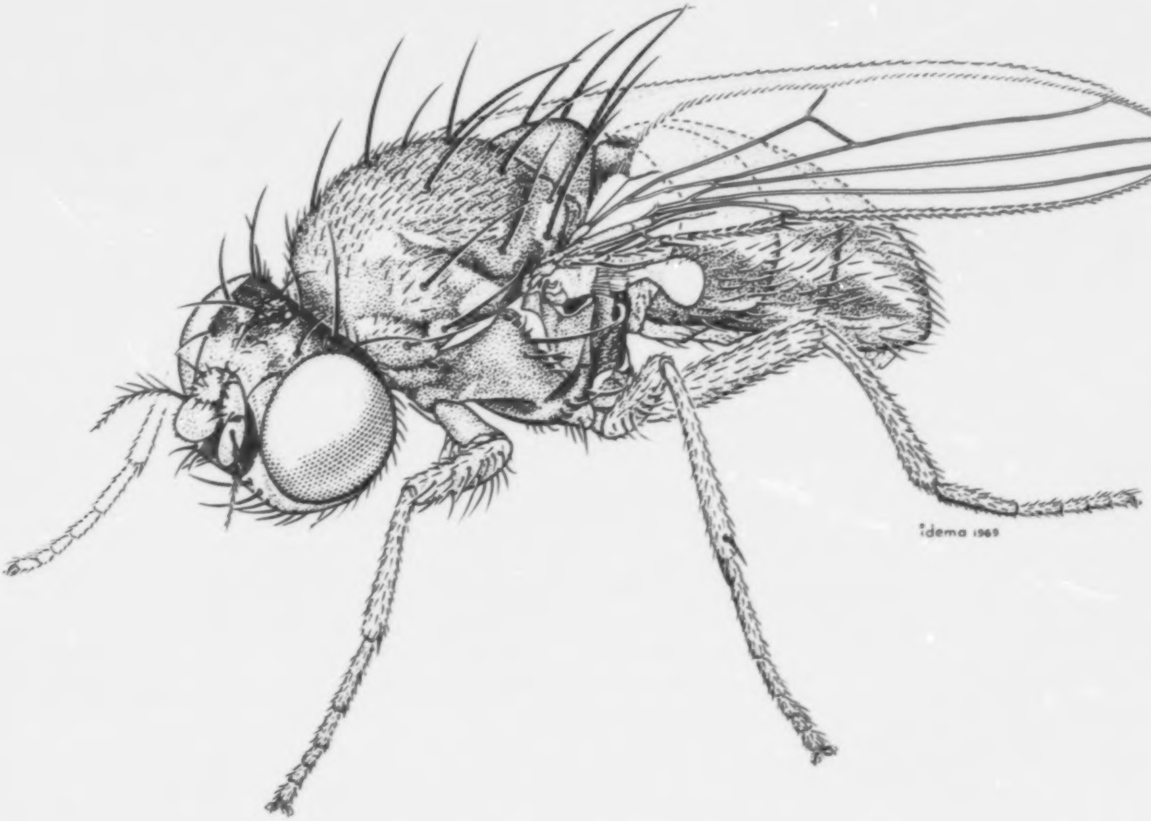
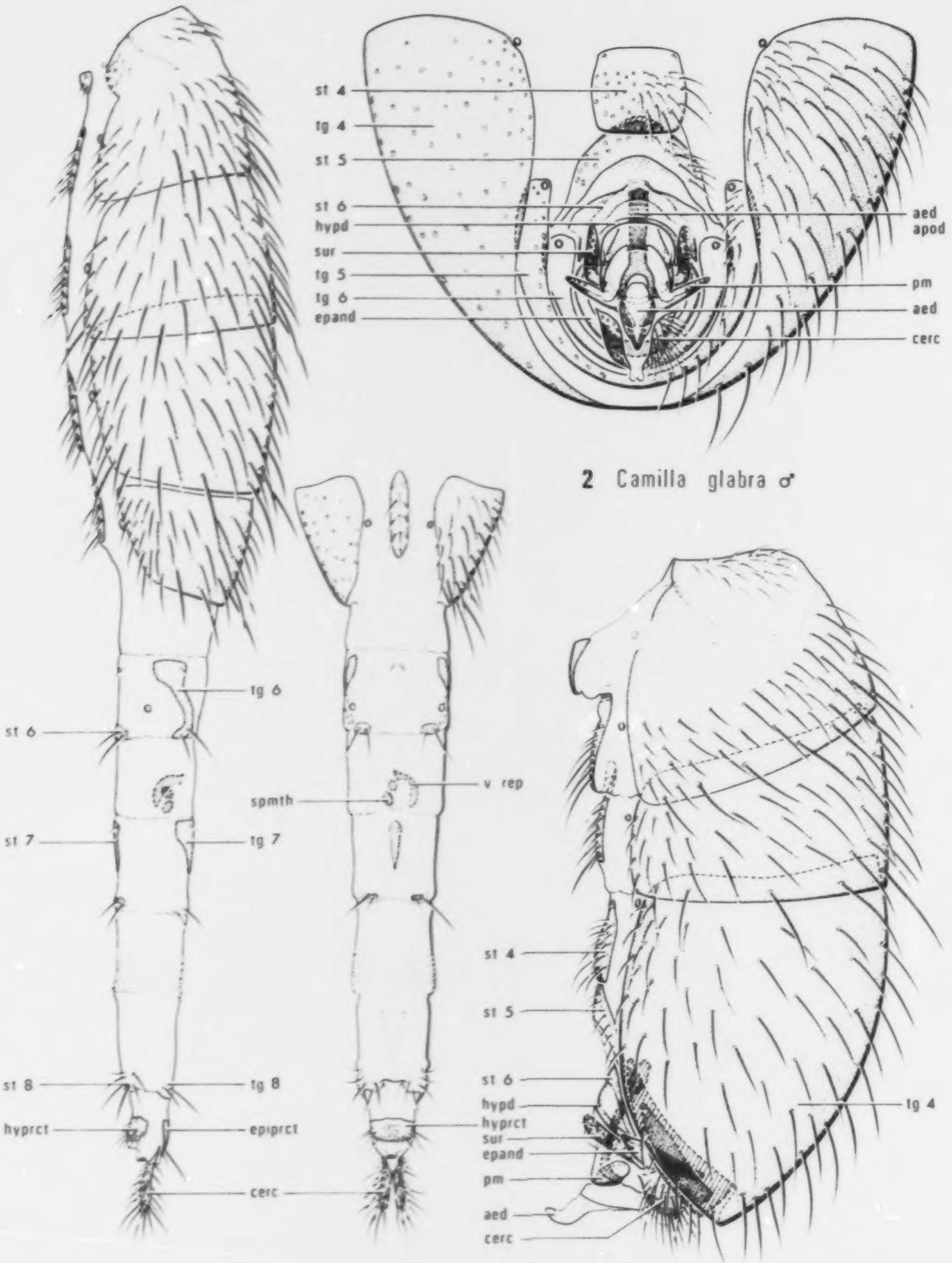


Fig. 97.1. Adult male of *Camilla glabra* (Fallén).

Small drosophilid-like flies (Fig. 1), 3–4 mm long, mostly shining black in color, with yellowish hyaline wings. Only one species, *Camilla glabra* (Fallén), known in Nearctic region, probably accidentally introduced from Europe.

Adult. Head: almost twice as high as long (Fig. 1), with strong black bristles. Frons with sides almost parallel; mid portion with a few scattered setulae; one reclinate orbital bristle arising in middle of orbital plate and one proclinate orbital bristle arising a short distance below it; a tiny reclinate setula located between these bristles; ocellar bristles and inner and outer vertical bristles subequal in size; postocellar bristles cruciate, about same size as reclinate orbital bristle. Lunule concealed. Face slightly depressed, uniformly sclerotized in middle, without median carina; parafacial very narrow. Clypeus transversely linear; gena about as broad as width of first flagellomere, with a row of seven or eight subvibrissal setae; vibrissa present, only slightly stronger than adjacent subvibrissal setae. Compound eye vertically oval, practically bare. Antenna short; pedicel somewhat bulbous, with apex extending into base of first flagellomere as in Drosophilidae, with a rather distinct longitudinal seam as in the Drosophilidae; first flagellomere elongate oval, sharply decumbent as in the Drosophilidae, not much longer than pedicel; arista plumose, with basal five or six rays on dorsal side much longer than remaining ones and ventral rays very short throughout. Mouthparts and palpus normal.

Thorax: uniformly shining black (Fig. 1). Scutum strongly arched as in the Drosophilidae, finely setulose throughout; scutellum strongly convex. Chaetotaxy: one postpronotal, one presutural supra-alar, no presutural and two postsutural dorsocentral, one postsutural supra-alar, two postalar, and two notopleural bristles present; prescutellar acrostichal bristles absent; scutellum with two pairs of bristles; proepisternal bristle moderately strong; proepimeral bristle absent; anepisternum with one strong bristle near upper third of hind margin and additional fine setulae on all sides of it; katepisternum with one large and one small bristle on upper posterior corner, and with additional fine setulae; pleural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2 Camilla glabra ♂

3 Camilla glabra ♀ **4** Camilla glabra ♀ **5** Camilla glabra ♂

Figs. 97.2–5. Abdomen of *Camilla glabra* (Fallén): (2) male terminalia, ventral view; (3) left lateral view of female abdomen; (4) ventral view of female terminalia; (5) left lateral view of male abdomen.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; epiprct, epiproct; hypd, hypandrium; hyprct, hypoproct; pm, paramere; sg, segment; spmth, spermatheca; st, sternite; sur, surstylus; tg, tergite; v rep, ventral receptacle.

sclerites otherwise bare. Prosternum broader than long, extending laterally in front of coxa but not really fused with pleuron, bare. Metasternal area bare. Fore femur with numerous rather strong posterior bristles and a stout peg-like ctenidial bristle near apex on anteroventral surface; preapical dorsal tibial bristle developed on mid tibia. Wing rather long and narrow, nearly three times as long as broad; anal angle rounded; alula small; C extending weakly to M_{1+2}, with both a humeral break and a subcostal break; seven or eight small widely spaced costal spines present; Sc incomplete; crossvein r-m meeting M_{1+2} at basal one-fourth of cell dm; cell dm and cell bm confluent; A_1 and cell cu*p* absent.

Abdomen: mostly shining black, with weak metallic reflections. Tergite 4 very elongate in both sexes, in male (Fig. 5) as long as combined length of previous three tergites, somewhat shorter in female (Fig. 3). Spiracle 7 absent in both sexes.

Male with tergites 5 and 6 much reduced (Fig. 2), and with tergites 7 and 8 atrophied; sternites 6 and 7 mostly atrophied; spiracles 5 and 6 situated in lateral extremities of corresponding tergites. Epandrium very short, band-like in side view. Surstylus rather long and slender, freely articulating with lateral extremities of epandrium, without teeth or strong bristles. Cerci small and membranous. Hypandrium narrowly U-shaped; gonopods and aedeagal guide forming a U-shaped process within arms of hypandrium about anterior base of aedeagus; parameres articulating with posteroapical extremities of gonopods and projecting at each side of aedeagus; aedeagus very short, little more than a sclerotized basal ring with a membranous eversible apical portion; aedeagal apodeme rod-like, mostly free from hypandrium, V-shaped at base, and with a swollen anterior apex.

Female (Figs. 3, 4) with sclerites of segments 6 and 7 mostly atrophied. Ovipositor mostly membranous; cerci rather long and slender. Two spermathecae present, each very small, oval, extremely weakly sclerotized, and scarcely pigmented.

Biology and behavior. The immature stages are unknown. Adults of *Camilla glabra* (Fallén), the only species known in the New World (McAlpine 1960), have been captured at the entrances to rabbit burrows, and a few have been reared from mouse nests in Britain (Collin 1956). In Canada this species is most often taken at windows. *Katacamilla cavernicola* Papp was collected from a cave in southwest Africa (Papp 1978).

Classification and distribution. The family is most closely related to the Curtonotidae and Drosophilidae; at one time it was included with the Drosophilidae. It consists of two living genera, *Camilla* Haliday and *Katacamilla* Papp; *Camilla* contains less than a dozen species from Eurasia and the adjoining Mediterranean subregion. *Katacamilla* contains one species, *K. cavernicola* Papp. One fossil species, *Protocamilla succini* Hennig from Baltic amber, is known (Hennig 1965).

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EPHYDRIDAE

98

WILLIS W. WIRTH, WAYNE N. MATHIS, AND J. R. VOCKEROTH

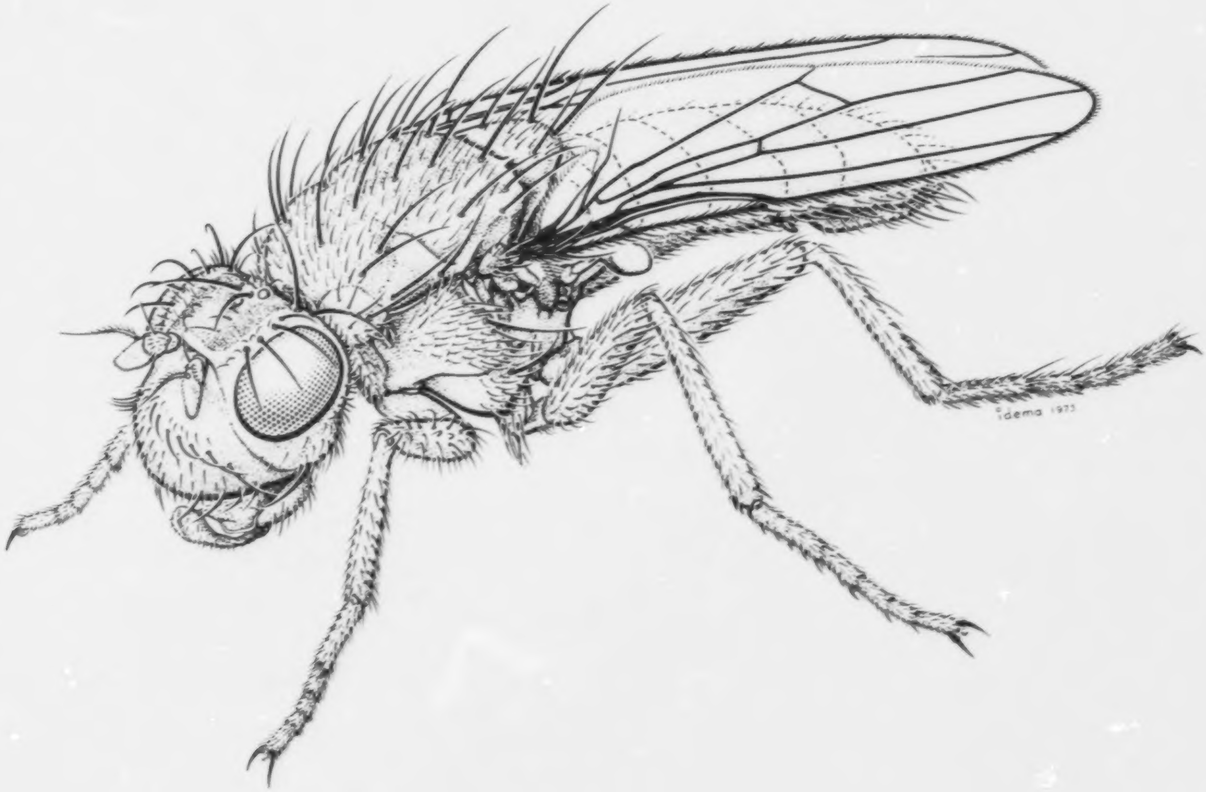


Fig. 98.1. Male of *Ephydra* (*Ephydra*) *riparia* Fallén.

Small to moderate-sized flies (Fig. 1), 1–11 mm long, usually dull and dark in color, but unusually diverse in body structure, vestiture, and ornamentation, making this family difficult to characterize; female usually larger than male. Pseudopostocellar bristles divergent or lacking. Arista bare, pubescent, or pectinate; rays present on dorsum only, except in *Asmeringa* Becker and in some *Ptilomyia* Coquillett. Wing with humeral and subcostal breaks; Sc rudimentary; R_1 merging with C before middle of wing; cells bm and dm not separated by a crossvein; cell cup absent. Anepisternum setulose. Preapical dorsal bristle lacking on fore and hind tibiae. Immature stages mostly aquatic or associated with aquatic habitats.

Adult. Head: eye usually bare, infrequently pubescent; shape round, subellipsoidal, or pyriform. Ocellar triangle often raised in relief; ocelli arranged to form an isosceles or equilateral triangle. Frons usually wider than long; frontal vitta often differentiated, shining; fronto-orbital plate mostly dull. Chaetotaxy of frons variable in size, orientation, and composition of bristles; true postocellar bristles absent, the bristles usually so designated being enlarged ocellar hairs, usually arising behind the posterior ocelli, and here called pseudopostocellar bristles (see McAlpine, Ch. 116); proclinate and reclinate fronto-orbital bristles often present in Psilopinae and Hydrelliinae, although one or both frequently lacking; fronto-orbital bristles in Parydrinae and Ephydrinae lateroclinate, strongly so in Ephydrinae. Antenna short; arista dorsal, frequently pectinate on dorsal surface, rarely plumose, otherwise pubescent or bare, inserted toward base of first flagellomere, rudimentary in *Lipochaeta* Coquillett (Fig. 27); pedicel often bearing one distinctly larger sometimes spine-like seta dorsoapically; antennal bases approximate except in *Lipochaeta*. Face extremely variable in form, setulose and frequently arched, protruding in Ephydrinae; vibrissal and subvibrissal setae present but quite varied in number, length, strength, and position and here collectively referred to as facial bristles or setae. Clypeus concealed or exposed, sometimes only partially exposed through ventral facial emargination or as a moderately wide band; subcranial cavity large and gaping when clypeus bandlike; tubercles, carinae, and other facial sculpturing frequently evident; gena high to barely evident, setulose or bare, often with one larger seta. Mouthparts large or small; when large, usually pendulous and bulbous, with well-developed prementum.

Thorax: appearance totally or in varying combinations shiny, metallic, or dull, and densely pruinose; integument sculptured (especially in Parydrinae), or entirely smooth. Chaetotaxy variable; when setae present, situated in typical setal positions. Scutellum variable; drawn out, bulbous, and beetle-like in *Peltopsilopa* Hendel (Neotropical); lateral or apical protuberances or both present in many species of Parydrinae. Legs generally similar, although fore femur and mid femur frequently with ventral armature; mid tibia sometimes with dorsal bristles and preapical dorsal bristle; foreleg of *Ochthera* Latreille raptorial (Fig. 63); claws variable in length and curvature; empodia and pulvilli variable, frequently lacking or reduced in Ephydrinae. Wing (Figs. 50–59) usually well-developed but sometimes reduced, entirely hyaline to maculate, with degree of maculation, pattern of venation, and general wing shape variable and of considerable taxonomic value; C usually extending to M, but sometimes only to R_{4+5}; C with both humeral and subcostal breaks; subcostal break sometimes with a strong incision; C spinose in a few exotic species; Sc incomplete; crossveins r-m and dm-cu present; crossvein bm-cu absent; CuA_2 and A_1 vestigial or absent, never forming a closed cell cu*p*; A_2 absent. Alula large and protruding to small and narrow. Halter variable in color, from white to black.

Abdomen: integument usually uniform, although varying considerably from species to species; integument smooth, hairless, and shiny in many members of Psilopinae and Parydrinae, e.g. in some species of *Athyroglossa* Loew, *Hyadina* Haliday, *Psilopa* Fallén, and related genera; pitted in *Gastrops* Williston; finely sculptured in *Pelina* Haliday; and pruinose in more typical members of Hydrelliinae and Ephydrinae. Exposed segments varying in number and conformation, mostly subequal but differing considerably in specimens of *Allotrichoma* Becker, *Microlytogaster* Clausen (Fig. 65), *Hyadina*, and *Pseudohecamede* Hendel. Setulae when present uniformly distributed or with larger setae along lateral and posterior margins; markedly larger setae on terminal segment in species of some genera of Psilopinae (e.g. *Clasiopella* Hendel); a row of spine-like setae along posterior margin of tergite 4 in males of some species of *Notiphila* Fallén, with segment 5 produced into a process terminating in two or three larger bristles. Male commonly with five exposed segments; female with six or seven. Abdominal spiracles 2–5 and sometimes 1 and 6 located in tergites rather than in pleural membrane. Male terminalia (Fig. 66) symmetric, consisting of epandrium, hypandrium, frequently paired surstyli (usually along ventral margin of epandrium), aedeagus, aedeagal apodeme, and an assortment of other processes such as gonopod, paramere, and hypandrial projections; sclerites of segments 6–8 lacking except for spiracle 6; all these structures varying in shape, number of additional processes or subdivisions, vestiture, and position, making them prime characters for taxonomic use. Female terminalia (Fig. 67) telescoped within first four or five segments except during oviposition, and consisting of segments 6–9 plus paired cerci; ventral margins of apical segments often bearing additional spines and setae that presumably aid in mating or oviposition; two spermathecae usually present, rudimentary and probably nonfunctional (Sturtevant 1926); ventral receptacle heavily sclerotized, functioning in place of spermathecae (many illustrated by Tenorio 1980).

Egg. White to grayish white, 0.33–1.30 mm long, 0.14–0.49 mm wide, usually ellipsoidal ovoid, often with a flattened surface, although contours generally symmetric except near ends (Fig. 68). Ends bluntly rounded to subbulbous; micropylar end sometimes drawn out, forming an elongate process or horn of varying length (*Paracoenia* Cresson, some species of *Ochthera*), and usually with a very small narrowly campanulate nipple. Chorion microreticulate to deeply rugose, sometimes with longitudinal ridges; ridges sometimes forked, as in *Hydrellia* Robineau-Desvoidy and *Discocerina obscurella* (Fallén).

Larva. First instar metapneustic, as small as 0.42 mm (*Discocerina obscurella*); second and third instars amphipneustic; third instar reaching 12.83 mm (*Cirrula gigantea* Cresson); instars similar except for size. General shape and ornamentation varying considerably (Figs. 69, 70), dorsoventrally flattened to cylindrical, sometimes with lateral branched processes (*Discomyza* Meigen) or with elongate respiratory tubes bearing terminal spiracles (especially members of Ephydrini) and sometimes accessary filaments (*Ephydra cinerea* Jones). Up to eight pairs of abdominal prolegs present (Ephydrini), each with two or three rows of hooks; last pair of prolegs larger, with opposable hooks; creeping welts sometimes present (*Notiphila caudata* Fallén), or apparent ambulatory processes lacking. Mandibles present, not joined together behind mouth opening except in species of *Hydrellia*, in which they are entirely fused as is their hypopharyngeal sclerite. Integument usually transparent, with numerous spinules of varying sizes. General facies, position, and strength of integumental processes and spiracular and cephalophargyngeal structures of considerable taxonomic value.

Puparium. Roughly similar in shape to third instar larva, although more compact, darker in color (light yellow to grayish brown), hardened, and with some distinctive features such as a dorsal cephalic cap.

Biology and behavior. The Ephydridae, or shore flies, are mainly beneficial, providing food for wildlife, especially waterfowl, that inhabit the marshes where these flies so commonly breed. In a few areas, however, the leaf or stem mines of *Hydrellia* become extensive enough to damage crops of watercress, rice, barley, and other irrigated cereals (Grigarick 1959). Lange (1954) estimated that *Hydrellia griseola* (Fallén) destroyed 10–20% of the Californian rice crop in 1953. A species of *Notiphila*, also, was reported to damage the roots of rice in Japan (Koizumi 1949).

Aquatic and semiaquatic habitats are typical for the family. However, several genera have evolved structural and behavioral modifications that adapt them for remarkably divergent habitats. The greatest of these evolutionary specializations is the adaptation to extremes in salt concentration. Although many shore flies frequent the muddy margins of freshwater environments, their numbers or their biotic importance do not compare to those occurring in maritime marshes, tidal salt pools, or the salt and alkaline lakes of arid regions. The relative isolation and reduced interspecific competition in such habitats have resulted in the evolution of very distinctive, specialized genera and species.

Most shore fly larvae feed by filtering microorganisms from the surrounding semiliquid medium. The food sources vary considerably, however, depending on the feeding habit. Most larvae are microphagous on bacteria, unicellular algae, and yeasts, although some prefer dead and decaying animal tissue. A few exist in excrement. The larvae of some species of *Clanoneurum* Becker, *Hydrellia*, *Lemnaphila* Cresson, and *Psilopa* are leaf miners; the larva of *Trimerina madizans* (Fallén) feeds as a parasitoid within egg cocoons of certain marsh-inhabiting spiders; and the larvae of *Ochthera* spp. are predators, feeding primarily on the immature forms of Chironomidae.

The paucity of published information on immature stages precludes their further characterization or the construction of adequate keys. Hennig (1952) summarized all data then available and attempted a partial key. Significant studies published since Hennig's compilation include Wirth (1954, *Paracoenia* (*Thiomyia* Wirth)), Nielsen *et al.* (1954, *Parydra* Stenhammar), Eastin and Foote (1971, *Notiphila caudata* species group), Deonier (1971, *Hydrellia*; 1974, *Scatophila* Becker), Foote and Eastin (1974, *Discocerina* Macquart), Simpson (1975, *Ochthera*; 1976*a*, *Ephydra* Fallén), Deonier and Regensburg (1978, *Parydra*), Busacca and Foote (1978, *Notiphila*), Deonier *et al.* (1979, *Notiphila*), Mathis and Simpson (1981, *Cirrula* Cresson and *Dimecoenia* Cresson), Tenorio (1980, Hawaiian spp.), Foote (1981*a*, *Lytogaster* Becker; 1981*b*, *Pelina* Haliday; 1982, *Setacera* Cresson; 1983, *Nostima* Coquillett), and Zack (1983, *Paracoenia*).

Feeding habits of adults likewise vary considerably, but most are microphagous on microscopic algae (Foote 1977, 1981*a*, 1981*b*), dinoflagellates, and other unicellular forms. Brock and co-workers (1969) demonstrated conclusively that both adults and larvae of *Ephydra buresi* Cresson and *Paracoenia bispinosa* (Coquillett) (misinterpreted as *P. turbida* (Curran)) ingest, digest, and assimilate bacteria and blue green algae found growing in the algal mats that form on the effluent of some hot springs in Yellowstone National Park.

A major digression from the microphagous feeding habit occurs in species of *Ochthera*. The nonspecific, predatory behavior of members of this genus is well documented (Simpson 1975). Prey of *Ochthera* varies from bloodworms captured by excavating the substrate to adults of most small insects that can be overpowered.

Species of many other genera are polyphagous, sometimes even cannibalistic, scavenging on dead or dying insects, and others feed on nectar and leaf epidermis besides having the typical microphagous habit. These habits have been reported in part or totally for adults of *Hydrellia* (Deonier 1971), *Notiphila* (Dahl 1959), *Hecamede* Haliday (Ardö 1957), and *Helaeomyia* Cresson (Thorpe 1930).

Although the mating behavior of ephydrids has been widely studied, generalization is difficult. Dahl (1959) distinguished six phases while studying the mating behavior of Scandinavian shore flies. Deonier (1971) found it more flexible simply to recognize epigamic and gamic behavior for describing the mating habits of various *Hydrellia* spp. Dahl (1959) observed males of *Notiphila caudata* defending territories established for courtship and mating. A defending male repulses an intruding conspecific male by orienting his spine-tipped abdomen in the direction of the intruder and attempting to overturn him. If the intruder is a female, the male immediately begins courtship.

Simpson (1976*b*) summarized observations regarding oviposition behavior. Noteworthy among these is the pattern followed by females of *Ephydra cinerea* and *Ephydra hians* Say. Wirth (1971) observed that "... females enter the water by walking down a stick or other emergent object which they grasp with their long straight claws, a bubble of air enclosed under the wings. They walk around on the bottom algae or other firm material, hanging on with their claws, and when ready to surface they merely let go, and rise with the air bubble which bursts at the surface leaving them standing high and dry."

The basic work on shore fly ecology is Dahl's study (1959) of the Scandinavian fauna. Since then several excellent papers treating North American taxa have appeared. These include Deonier (1965), Collin (1975), and Simpson (1976*b*). The papers by Scheiring and Foote (1973), and by Simpson (1976*b*), are exceptionally good, summarizing data for several species.

Oldroyd (1964) aptly summarized the state of affairs of shore fly biology: "Evidently we are seeing in the Ephydridae a family of flies in the full flower of its evolution, and as such they offer attractive material for study, not only to the dipterist, but also to students of insect physiology and behaviour."

Classification and distribution. The basic classification of the Ephydridae, first laid down by Haliday (1839) and later modified and elaborated by Loew (1860) and Becker (1896, 1926), divided the family into three subfamilies: Ephydrinae, Notiphilinae, and Hydrelliinae. Cresson gradually evolved a classification differing somewhat from theirs, which ultimately recognized the four subfamilies we adopt here: Psilopinae, Hydrelliinae, Parydrinae, and Ephydrinae. In 1942, 1944, 1946, and 1949 (posthumously), Cresson published a series of synopses for the first three subfamilies, in which he presented keys for the identification of tribes, genera, and species, plus complete up-to-date information on synonymy, distribution, and status of all species known to him. Sturtevant and Wheeler (1954) presented an excellent revision of the North American Parydrinae and Ephydrinae, and of a few genera in the other subfamilies, to supplement Cresson's synopses. Wirth and Stone (1956) published keys to the North American genera and the Californian species, and Deonier (1964) presented keys to the genera and species occurring in Iowa. The last two papers are not referred to in the generic key below.

Hennig (1958) placed the Camillidae nearest the Ephydridae but later (1971) discarded this hypothesis after discovering an antennal character linking the Camillidae with the Drosophilidae and the Curtonotidae. Hennig (1971) then suggested that the Camillidae, Drosophilidae, and Curtonotidae, which he grouped under the name Drosophilidea, formed the sister group of the Ephydridae plus Diastatidae, which he named the Ephydridea. The basis for the sister-group relationship between Ephydridae and Diastatidae is the presence of a well-sclerotized female ventral receptacle that functions in place of the reduced spermathecae (Sturtevant 1926). Griffiths (1972) modified Hennig's proposal, placing the genus *Diastata* Meigen alone as the sister group of the Ephydridae because only this genus in the Diastatidae is known to possess the female ventral receptacle as described above. However, Griffiths also proposed the combination of *Diastata* with Ephydridae as a single family and the formation of a new family, the Campichoetidae, for the remaining genera of Diastatidae.

In our opinion, this action was premature; regardless of the sister-group relationship, the Ephydridae as traditionally recognized remain a convenient, easily recognized, monophyletic assemblage. We have identified several autapomorphies for the Ephydridae *sensu stricto* (listed below) that clearly establish the monophyly and divergence of that family from *Diastata*. Further, the monophyly of Griffiths' family Campichoetidae lacks confirmation (*Euthychaeta* Loew was not studied), and it could prove to be paraphyletic.

Characters autapomorphic to the Ephydridae are: postocellar setae absent; sclerites of abdominal segments 6–8 absent in the male except for the sixth spiracle; ejaculatory apodeme absent; cell cu*p* absent and vein A_1 rudimentary; abdominal spiracles 2–5 and sometimes 1 and 6 situated within tergites; and cells bm and dm not separated by a crossvein.

Apparently there are no fossil records of Ephydridae. According to Hennig (1965) the Baltic amber Ephydrinidae (=Ephydridae) mentioned by Loew belong in the present-day family Camillidae.

More than 1300 species of Ephydridae have been described, of which 425 species and 68 genera occur in the Nearctic Region. Shore flies occur in all major zoogeographic realms and on most oceanic islands, and because most are able flyers, endemism is low at the generic level. Only seven genera appear to be limited to the Nearctic: *Callinapaea* Sturtevant & Wheeler, *Microlytogaster* Clausen, *Pelignellus* Sturtevant & Wheeler, *Pelignus* Cresson, *Pseudohyadina* Clausen, *Rhinonapaea* Wirth, and *Trimerinoides* Cresson.

Key to genera

1. Median facial area and lower facial margin without setae; facial bristles inserted in more or less vertical series, parallel with parafacial. Subcranial cavity small to large (Figs. 2–37) 2

Median facial area and lower facial margin setose, the latter often with long bristles; insertions of facial series of bristles convergent above. Subcranial cavity large and cavernous (Figs. 38–40) .... EPHYDRINAE 64

2. Presutural or sutural dorsocentral bristle inconspicuous or absent (Fig. 48) 3

Presutural or sutural dorsocentral bristle present, conspicuous (Fig. 49) 41

3. Arista pectinate, with branches sometimes pale and difficult to discern (Figs. 2–24) 4

Arista bare to macropubescent, or rudimentary; if arista pectinate, hairs shorter than one-half width of first flagellomere (Figs. 25–37) 36

4. Foreleg raptorial; fore femur greatly enlarged; fore tibia ending in a spur (Fig. 63) .... PARYDRINAE, in part .... **Ochthera** Latreille

13 spp.; widespread; Clausen 1977

Foreleg normal; fore femur slender; fore tibia not ending in a spur 5

5. C short, extending only to R_{4+5}. Face with a distinct vertical carina (Fig. 2) .... PARYDRINAE, in part .... **Brachydeutera** Loew

3 spp.; widespread; Wirth 1964

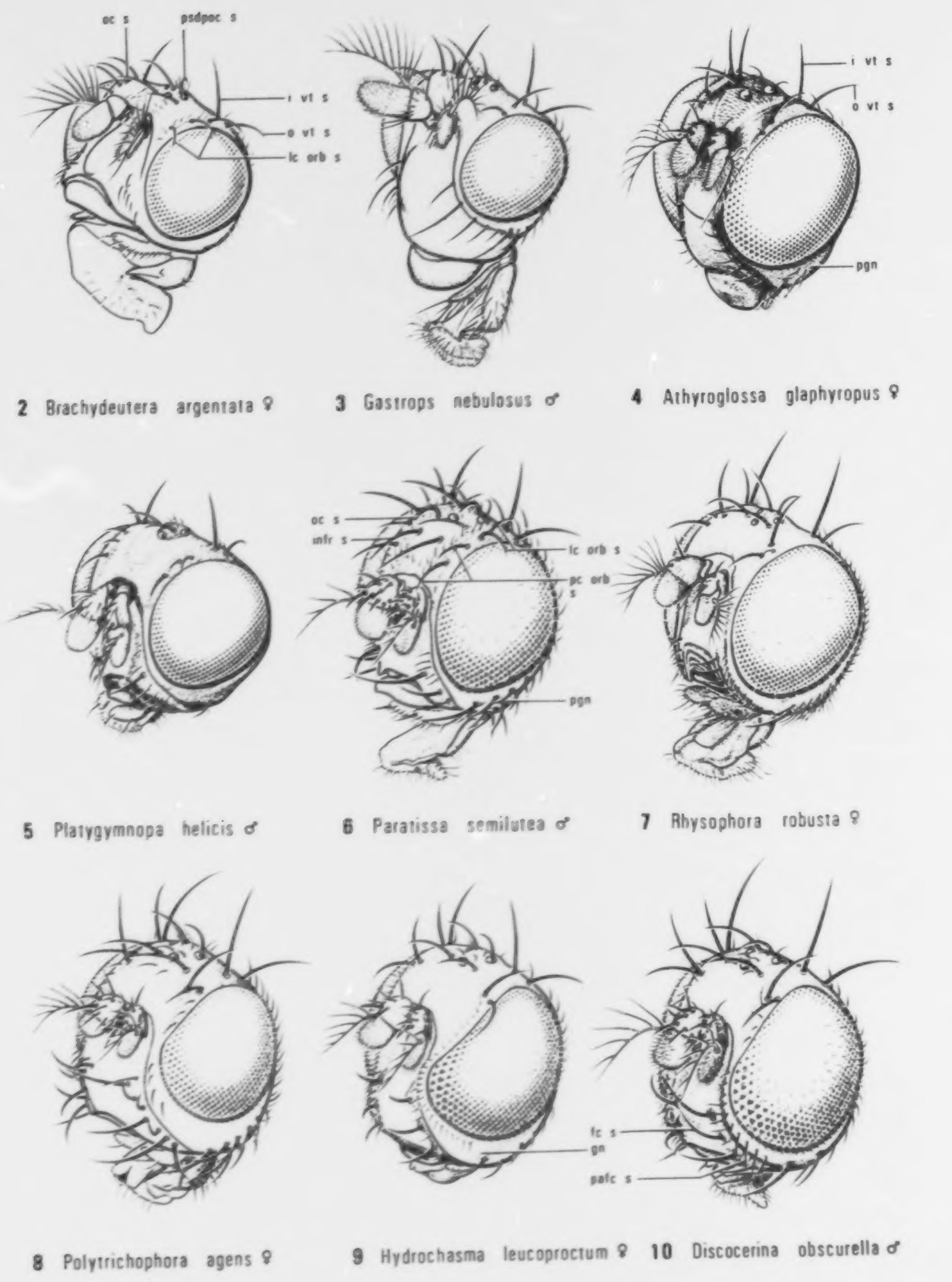
C long, extending to M. Face without a distinct vertical carina 6

6. Upper half of face conspicuously swollen; head in anterior view subtriangular; eyes distinctly bulging (Fig. 3) .... PARYDRINAE, in part .... **Gastrops** Williston

2 spp.; eastern U.S.A., Neotropical; Wirth 1958

Upper half of face not distinctly swollen; head not triangular; eyes not bulging (Figs. 4–24) .... PSILOPINAE, in part 7

7. Posterior margin of postgena meeting occiput at acute angle; postgena with fine pale setulae (Figs. 4, 5). Mostly or entirely shiny black species, with setation much reduced 8



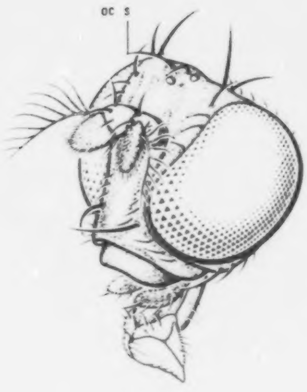
2 Brachydeutera argentata ♀ 3 Gastrops nebulosus ♂ 4 Athyroglossa glaphyropus ♀

5 Platygymnopa helicis ♂ 6 Paratissa semilutea ♂ 7 Rhysophora robusta ♀

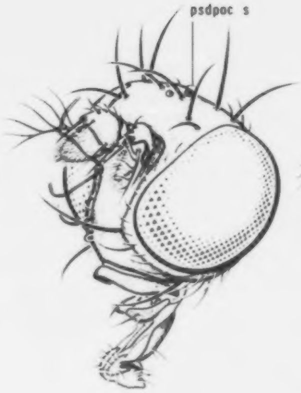
8 Polytrichophora agens ♀ 9 Hydrochasma leucoproctum ♀ 10 Discocerina obscurella ♂

Figs. 98.2–10. Heads: (2) *Brachydeutera argentata* (Walker); (3) *Gastrops nebulosus* Coquillett; (4) *Athyroglossa glaphyropus* Loew; (5) *Platygymnopa helicis* Wirth; (6) *Paratissa semilutea* (Loew); (7) *Rhysophora robusta* Cresson; (8) *Polytrichophora agens* Cresson; (9) *Hydrochasma leucoproctum* (Loew); (10) *Discocerina obscurella* (Fallén) (*continued*).

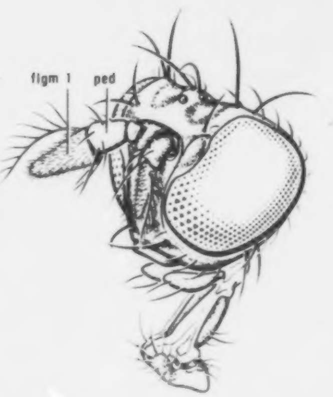
Abbreviations: fc s, facial seta; gn, gena; infr s, interfrontal seta; i vt s, inner vertical seta; lc orb s, lateroclinate orbital seta; oc s, ocellar seta; o vt s, outer vertical seta; pafc s, parafacial seta; pc orb s, proclinate orbital seta; pgn, postgena; psdpoc s, pseudopostocellar seta.



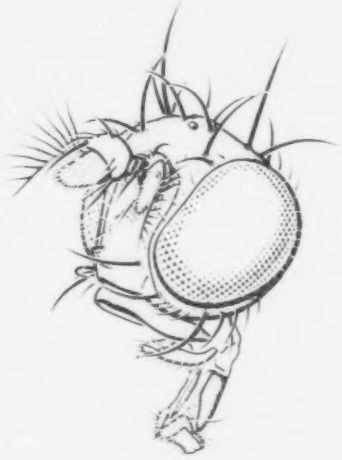
11 Cressonomyia aciculata ♀



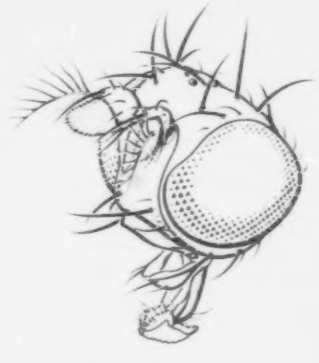
12 Leptopsilopa varipes ♂



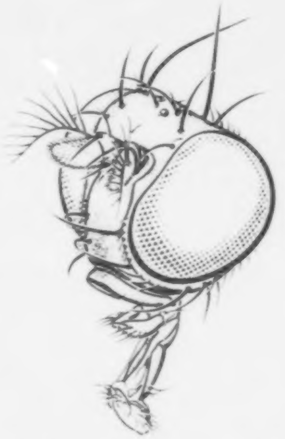
13 Ceropsilopa coquilletti ♂



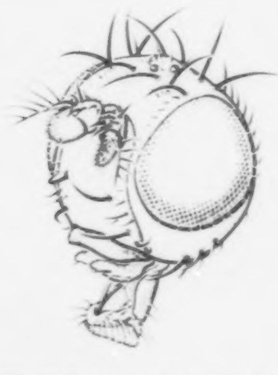
14 Clasiopella uncinata ♀



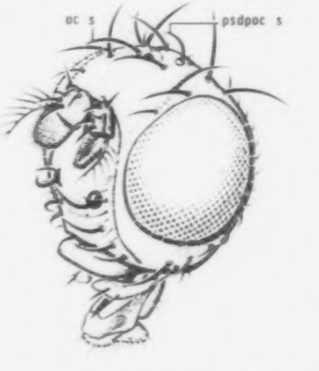
15 Psilopa flavida ♂



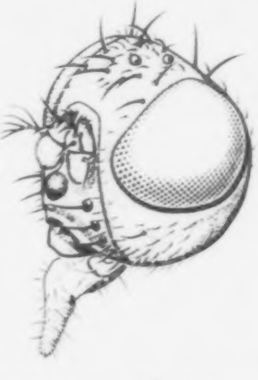
16 Psilopa sp. ♂



17 Diclasiopa lacteipennis ♂



18 Hecamedoides glaucellus ♂



19 Hecamede albicans ♀

Figs. 98.11–19. Heads (*continued*): (11) *Cressonomyia aciculata* (Loew); (12) *Leptopsilopa varipes* (Coquillett); (13) *Ceropsilopa coquilletti* Cresson; (14) *Clasiopella uncinata* Hendel; (15) *Psilopa flavida* Coquillett; (16) *Psilopa* sp.; (17) *Diclasiopa lacteipennis* (Loew); (18) *Hecamedoides glaucellus* (Stenhammar); (19) *Hecamede albicans* (Meigen) (*continued*).

Abbreviations: flgm, flagellomere; oc s, ocellar seta; ped, pedicel; psdpoc s, pseudopostocellar seta.

Posterior margin of postgena meeting occiput at obtuse and broadly rounded angle; postgena usually with coarse black setulae (Figs. 6–24). Shiny to dull species with setation usually well-developed 9

8. Face convex to transversely carinate (Fig.4). Outer vertical bristle as long as inner vertical bristle. Scutum as long as wide; scutellum subtruncate or rounded apically. Katepisternal bristle short but distinct. Abdomen only slightly flattened, with revolute margins .... ***Athyroglossa*** Loew

8 spp.; widespread; Wirth 1970

Face slightly and uniformly concave (Fig. 5). Outer vertical bristle one-half as long as inner vertical. Scutum slightly wider than long; scutellum nearly triangular. Katepisternal bristle absent. Abdomen strongly flattened, with sharp lateral margins .... ***Platygymnopa*** Wirth

1 sp., *helicis* Wirth; Canada, northern U.S.A.

9. Anterior and posterior notopleural bristles equidistant from notopleural suture (as in Fig. 45) 10

Posterior notopleural bristle much farther from notopleural suture than anterior bristle (as in Fig. 46) 29

10. R$_{2+3}$ close to C beyond end of R$_1$; crossvein dm-cu with sharp angle (Fig. 50) .... ***Clanoneurum*** Becker

1 sp., *americanum* Cresson; widespread

R$_{2+3}$ well-separated from C; crossvein dm-cu not angulate 11

11. Frontal vitta with a pair of strong proclinate interfrontal bristles well in front of ocellar bristles; frons with one large and one small lateroclinate upper fronto-orbital bristle and two large proclinate lower fronto-orbital bristles (Fig. 6) .... ***Paratissa*** Coquillett

1 sp., *semilutea* (Loew); Florida, Neotropical, coastal

Frontal vitta without interfrontal bristles although sometimes with ocellar bristles slightly in front of level of anterior ocellus; fronto-orbital bristles proclinate and reclinate but not lateroclinate (Figs. 7–18) 12

12. Face strongly and coarsely sculptured on at least lower half; facial bristles short, the longest at most three-fourths as long as its distance from opposing bristle (Fig. 7) 13

Face usually smooth, but if finely striate, the longest facial bristle at least as long as its distance from opposing bristle (Figs. 8–18) 14

13. Prescutellar acrostichal bristles absent; supra-alar bristle not longer than posterior notopleural bristle. Wing with at least crossvein dm-cu darkened, sometimes with extensive dark markings .... ***Discomyza*** Meigen

2 spp.; southern

Prescutellar acrostichal bristles present, strong; supra-alar bristle almost twice as long as posterior notopleural bristle. Wing unmarked .... ***Rhysophora*** Cresson

1 sp., *robusta* Cresson; eastern; Mathis 1977

14. Notopleuron with short setulae around anterior bristle; anterior notopleural bristle almost twice as far from postpronotal bristle as from posterior notopleural (Fig. 45). Parafacial setulose (Figs. 8–10) or bare 15

Notopleuron without setulae; anterior notopleural bristle at most one and one-third times as far from postpronotal bristle as from posterior notopleural bristle. Parafacial bare (Figs. 11–24) 17

15. Face with secondary series of dorsolaterally inclined bristles lateral to primary series (Fig. 8) .... ***Polytrichophora*** Cresson

4 spp.; widespread; Cresson 1942

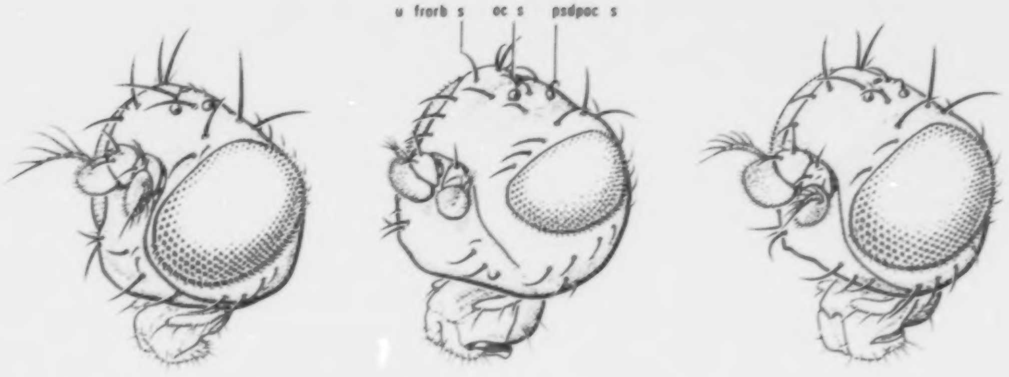
Face with secondary series of bristles absent or suggested only by medially inclined setulae (Figs. 9, 10) 16

16. Densely cinereous dull species. Gena and lower part of parafacial broad (Fig. 9) .... ***Hydrochasma*** Hendel

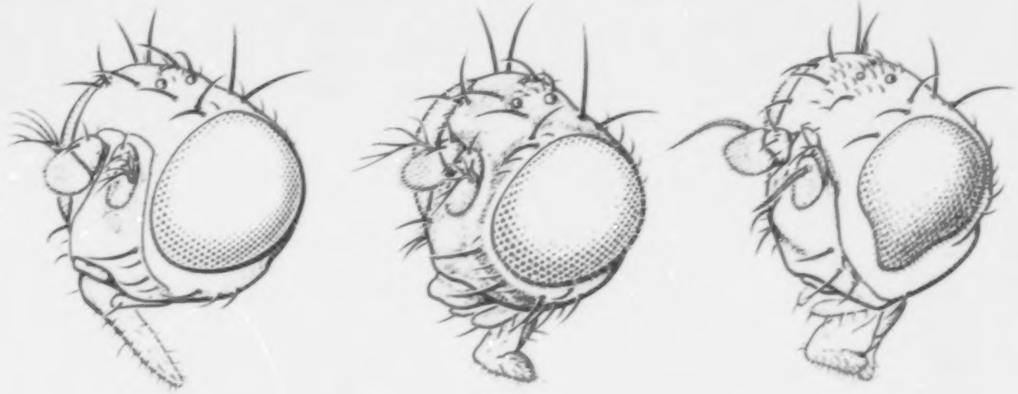
4 spp.; widespread; Cresson 1942

Shining to dark dull species. Gena and parafacial rather narrow (Fig. 10) .... ***Discocerina*** Macquart

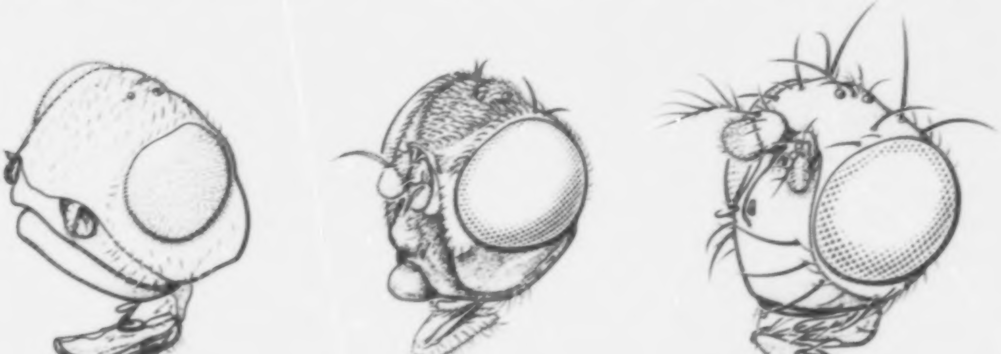
7 spp.; widespread; Cresson 1942



20 Ptilomyia mabelae ♀ **21** Pelignellus subnudus ♂ **22** Atissa pygmaea ♀



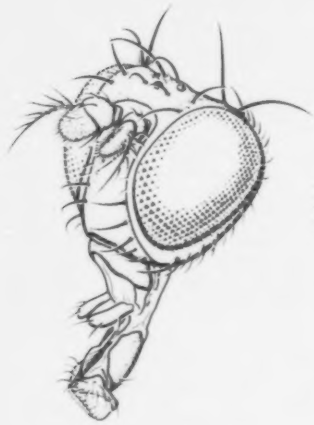
23 Pseudohecamede abdominalis ♀ **24** Diphuia nitida ♀ **25** Glenanthe interior ♀



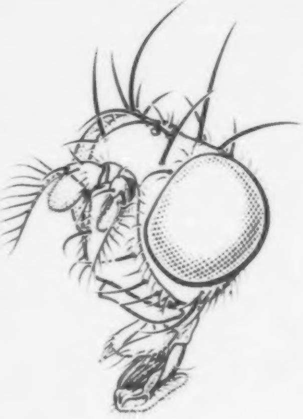
26 Lipochaeta slossonae ♂ **27** Mosillus tibialis ♂ **28** Ilythea spilota ♀

Figs. 98.20–28. Heads (*continued*): (20) *Ptilomyia mabelae* (Cresson); (21) *Pelignellus subnudus* Sturtevant & Wheeler; (22) *Atissa pygmaea* (Haliday); (23) *Pseudohecamede abdominalis* (Williston); (24) *Diphuia nitida* Sturtevant & Wheeler; (25) *Glenanthe interior* Chillcott; (26) *Lipochaeta slossonae* Coquillett; (27) *Mosillus tibialis* Cresson; (28) *Ilythea spilota* (Curtis) (*continued*).

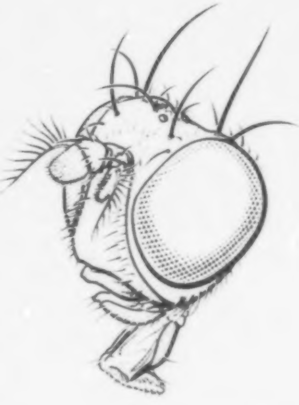
Abbreviations: oc s, ocellar seta; psdpoc s, pseudopostocellar seta; u frorb s, upper fronto-orbital seta.



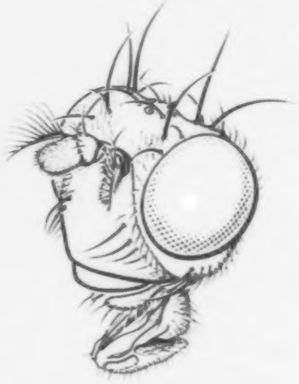
29 Hydrellia griseola ♀



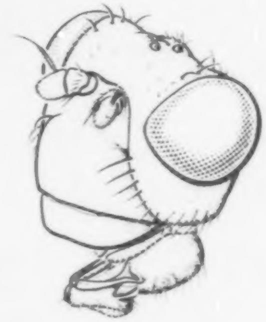
30 Notiphila (Dichaeta) caudata ♂



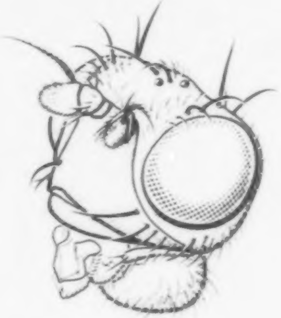
31 Notiphila (Dichaeta) scalaris ♂



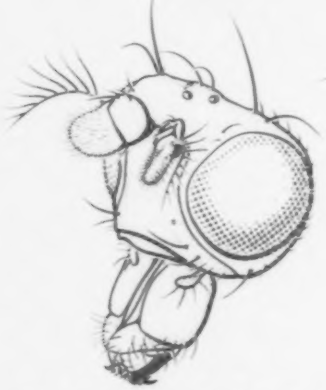
32 Paralimna (Phaiosterna) decipiens ♀



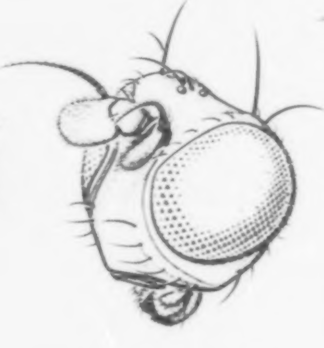
33 Parydra (Parydra) aquila ♂



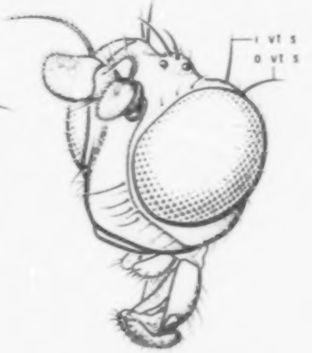
34 Parydra (Chaetoapnaea) parasocia ♀



35 Lemnaphila scotlandae ♀



36 Philygria debilis ♀



37 Hyadina binotata ♂

Figs. 98.29–37. Heads (*continued*): (29) *Hydrellia griseola* (Fallén); (30) *Notiphila (Dichaeta) caudata* Fallén; (31) *Notiphila (Dichaeta) scalaris* Loew; (32) *Paralimna (Phaiosterna) decipiens* Loew; (33) *Parydra (Parydra) aquila* (Fallén); (34) *Parydra (Chaetoapnaea) parasocia* Clausen; (35) *Lemnaphila scotlandae* Cresson; (36) *Philygria debilis* Loew; (37) *Hyadina binotata* (Cresson) (*continued*).

Abbreviations: i vt s, inner vertical seta; o vt s, outer vertical seta.

17. Prescutellar acrostichal bristles absent 18

Prescutellar acrostichal bristles present, distinct, varying from weak and close together to strong and far apart 19

18. Abdomen ovoid, with margins revolute. Wing with dark anteroapical spot .... ***Trimerinoides*** Cresson

1 sp., *adfinis* (Cresson); western

Abdomen slender, nearly parallel-sided, with margins sharp (Fig. 64). Wing without anteroapical spot .... ***Trimerina*** Macquart

1 sp., *madizans* (Fallén); widespread

19. Ocellar bristles inserted behind level of anterior ocellus; pseudopostocellar bristles lateroclinate, strongly divergent, sometimes very weak and scarcely distinguishable (Figs. 11–16) 20

Ocellar bristles inserted at or slightly in front of level of anterior ocellus; pseudopostocellar bristles proclinate, parallel or only slightly divergent, always moderately strong and distinct (Figs. 17, 18) 25

20. Wing yellowish with dark base. Fronto-orbital bristles strong (Fig. 11) or weak and hair-like. Halter blackish or pale .... ***Cressonomyia*** Arnaud

4 spp.; southern; Cresson 1942 (as *Plagiopsis* Cresson)

Wing usually unicolorous, but if maculate, dark areas not confined to wing base. Fronto-orbital bristles strong. Halter pale 21

21. Eye with abundant distinct hairs. Legs entirely blackish .... ***Helaeomyia*** Cresson

1 sp., *petrolei* (Coquillett); California, Neotropical

Eye with at most minute and scarcely distinguishable hairs (Figs. 12–16). Legs usually extensively yellow, at least with some tarsal segments distinctly yellowish 22

22. First tarsomere of foreleg slightly thickened, blackish in Nearctic species. Face with fine transverse striae, slightly carinate (Fig. 12) .... ***Leptopsilopa*** Cresson

4 spp.; widespread; Cresson 1942

First tarsomere of foreleg slender, yellow or blackish. Face smooth (Figs. 13–16) 23

23. Antenna with pedicel conical, broader apically, without dorsoapical lobe, with dorsoapical spine weak and at most one-third as long as first flagellomere; first flagellomere from two to four times as long as wide (Fig. 13) .... ***Ceropsilopa*** Cresson

7 spp.; southern, Neotropical; Cresson 1942

Antenna with pedicel short and subtriangular, with dorsoapical lobe, with dorsoapical spine strong and at least half as long as first flagellomere; first flagellomere at most twice as long as wide (Figs. 14–16) 24

24. Pseudopostocellar bristles moderately strong, slightly less than half as long as ocellar bristles (Fig. 14). Katepisternum with two bristles .... ***Clasiopella*** Hendel

1 sp., *uncinata* Hendel; Florida, Neotropical

Pseudopostocellar bristles very weak, at most one-third as long as ocellar bristles (Figs. 15, 16). Katepisternum with one bristle .... ***Psilopa*** Fallén

6 spp.; widespread; Cresson 1942

25. Arista truncate apically, not longer than first flagellomere (Fig. 41). Acrostichal setulae distinct, moderately strong, arranged in two regular rows of about five setulae each .... ***Pelignus*** Cresson

1 sp., *salinus* Cresson; Utah

Arista tapering, much longer than first flagellomere. Acrostichal setulae short and weak, often difficult to distinguish, numerous, arranged in four or more regular to irregular rows 26

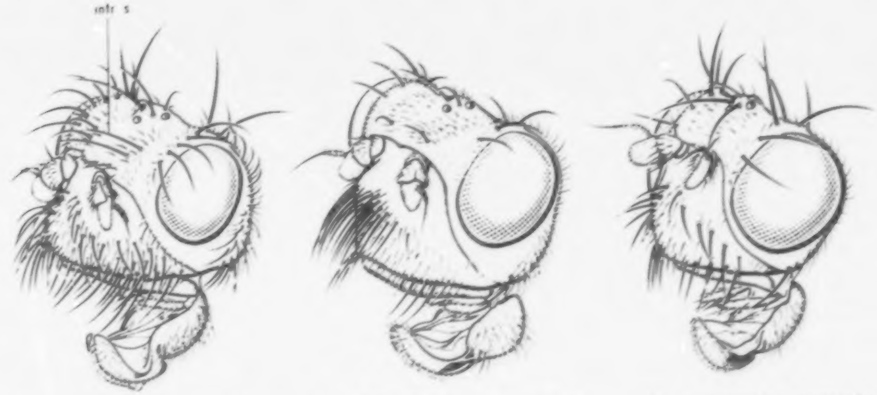
26. Costal margin of wing broadly darkened .... ***Nesopsilopa*** Mathis & Wirth

2 spp.; Florida; Mathis and Freidberg 1980

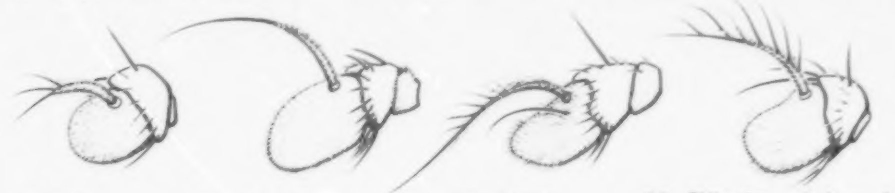
Wing unmarked 27

27. Supra-alar bristle strong, distinct, longer than posterior notopleural bristle. Face with upcurved seta at lower lateral extremity (Fig. 17) .... ***Diclasiopa*** Hendel

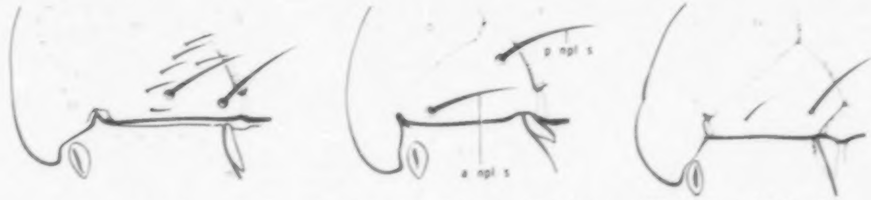
1 sp., *lacteipennis* (Loew); widespread



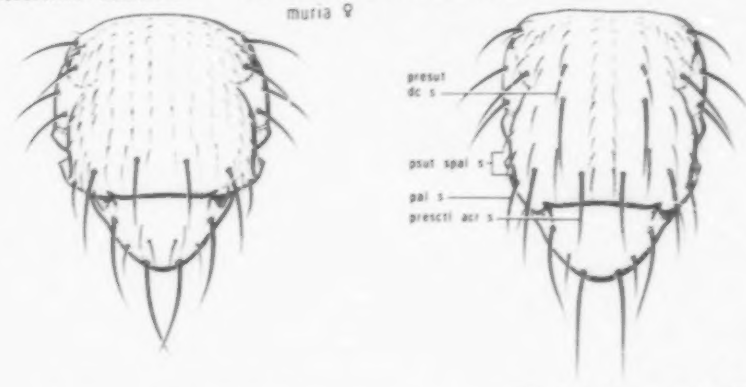
38 Ephydra (Hydropyrus) hians ♂ **39** Cirrula gigantea ♂ **40** Calocoenia platypelta ♀



41 Pelignus salinus ♀ **42** Pelina truncatula ♀ **43** Setacera pacifica ♂ **44** Philotelma alaskense ♀



45 Discocerina obscurella ♀ **46** Lamproscatella (Haloscatella) muria ♀ **47** Pelina biloba ♂



48 Allotrichoma simplex ♀ **49** Hydrellia griseola ♂

Figs. 98.38–49. Heads (*concluded*), antennae, and thoraces: heads of (38) *Ephydra* (*Hydropyrus*) *hians* Say, (39) *Cirrula gigantea* Cresson, and (40) *Calocoenia platypelta* (Cresson); antennae of (41) *Pelignus salinus* Cresson, (42) *Pelina truncatula* Loew, (43) *Setacera pacifica* (Cresson), and (44) *Philotelma alaskense* Cresson; dorsolateral views of notopleuron of (45) *Discocerina obscurella* (Fallén), (46) *Lamproscatella* (*Haloscatella*) *muria* Mathis, and (47) *Pelina biloba* Clausen; dorsal views of thorax of (48) *Allotrichoma simplex* (Loew) and (49) *Hydrellia griseola* (Fallén).

Abbreviations: a npl s, anterior notopleural seta; infr s, interfrontal seta; pal s, postalar seta; p npl s, posterior notopleural seta; presctl acr s, prescutellar acrostichal seta; presut dc s, presutural dorsocentral seta; psut spal s, postsutural supra-alar seta.

Supra-alar bristle very short or absent, if distinguishable distinctly shorter than posterior notopleural bristle. Face without upcurved seta at lower lateral extremity 28

28. Hind tibia with a preapical ventral spine-like bristle. Dull densely cinereous species. Face with three pairs of distinct bristles, the upper pair each on a distinct shiny papilla (Fig. 18) .... ***Hecamedoides*** Hendel

1 sp., *glaucellus* (Stenhammar); widespread

Hind tibia lacking a preapical ventral spine-like bristle. Mostly shiny species. Face with two or three pairs of distinct bristles, the upper pair not on papillae .... ***Ditrichophora*** Cresson

15 spp.; widespread; Cresson 1942

29. No distinct fronto-orbital or ocellar bristles evident; frons with small hairs only. Arista pubescent above and below. Tiny whitish species, with bristles reduced to fine hairs .... ***Asmeringa*** Becker

1 sp., *lindsleyi* Sturtevant & Wheeler; California

At least reclinate fronto-orbital and usually ocellar bristles well-developed (Figs. 19–24). Arista without pubescence or long hairs below. Species variable in size and color, but with distinct bristles 30

30. Face with a conspicuous shiny black median tubercle; gena broad, setulose; parafacial and frontal vitta setulose (Fig. 19). Scutellum with more than four marginal bristles .... ***Hecamede*** Haliday

1 sp., *albicans* (Meigen); northeastern U.S.A., coastal

Face without shiny median tubercle; gena narrow or broad, not setulose; parafacial and frontal vitta not setulose (Figs. 20–24). Scutellum with four marginal bristles 31

31. Upper fronto-orbital bristles situated in front of line between ocellar bristles; ocellar bristles behind level of anterior ocellus (Figs. 20–22) 32

Upper fronto-orbital bristles about in line with ocellar bristles; ocellar bristles before level of anterior ocellus (Figs. 23, 24) 34

32. Face conically prominent well above lower facial margin, with submedian pair of upcurved bristles (Fig. 20) .... ***Ptilomyia*** Coquillett

6 spp.; widespread; Sturtevant and Wheeler 1954

Face most prominent very near lower facial margin, without submedian pair of upcurved bristles (Figs. 21, 22) 33

33. Ocellar bristles small, equal to pseudopostocellar bristles; a pair of larger divergent interfrontal bristles present anterior to median ocellus (Fig. 21) .... ***Pelignellus*** Sturtevant & Wheeler, in part

1 sp., *subnudus* Sturtevant & Wheeler; California

Ocellar bristles strong, much stronger than pseudopostocellar bristles; no interfrontal bristles present anterior to median ocellus (Fig. 22) .... ***Atissa*** Haliday

2 spp.; widespread; Sturtevant and Wheeler 1954

34. Proboscis slender, geniculate, with lanceolate labella (Fig. 23) ... ***Pseudohecamede*** Hendel

3 spp.; southern Ontario, southern U.S.A.; Cresson 1942 (as part of *Allotrichoma*)

Proboscis normal, with fleshy labella (Fig. 24) 35

35. Shiny black species. Face with silvery spots and lines (Fig. 24) .... ***Diphuia*** Cresson

1 sp., *nitida* Sturtevant & Wheeler; New York, Florida

Dull pruinose grayish to brown species. Face not maculate .... ***Allotrichoma*** Becker

7 spp.; widespread

36. Ocellar and pseudopostocellar bristles absent or not distinguishable from the many short fine to coarse hairs present on the frontal vitta beside and in front of the ocellar triangle (Figs. 25–27) 37

Ocellar or pseudopostocellar bristles, or both, strong and distinct; frontal vitta without hairs beside and in front of the ocellar triangle (Figs. 21, 33–37) 40

37. Eye shaped like inverted pear, strongly narrowed below (Fig. 25) .... PSILOPINAE, in part .... ***Glenanthe Haliday***

3 spp.; widespread; Sturtevant and Wheeler 1954

Eye round to oval (Figs. 26, 27) 38

38. Antennae in deep cavities, separated from one another by almost twice their length; arista rudimentary, truncate. Inner and outer vertical bristles indistinguishable. Face very short (Fig. 26) .... PARYDRINAE, in part.... ***Lipochaeta*** Coquillett

1 sp., *slossonae* Coquillett; eastern and southern, Neotropical

Antennae in shallow cavities, separated from one another by much less than their length; arista normal, tapering. Inner and outer vertical bristles distinct. Face of normal length (Fig. 27) .... PSILOPINAE, in part....39

39. Body black, extensively shiny to subshiny. Face pitted or rugose, with shining tubercle on lower half, without keel between antennae. Frontal vitta with many fine hairs (Fig. 27) .... ***Mosillus*** Latreille

3 spp.; widespread; Wirth 1969

Body gray, heavily pruinose. Face smooth, without tubercle, with distinct rounded keel between antennae. Frontal vitta with about 10 coarse hairs .... ***Paraglenanthe*** Wirth

1 sp., *bahamensis* Wirth; Florida

40. Arista short, about equal to length of first flagellomere (Fig. 21). Prescutellar acrostichal bristles conspicuous (as in Fig. 48) .... PSILOPINAE, in part.... ***Pelignellus*** Sturtevant & Wheeler, in part

1 sp., *subnudus* Sturtevant & Wheeler; California

Arista long and slender (Figs. 33–37, 42). Prescutellar acrostichal bristles inconspicuous or lacking .... PARYDRINAE, in part....51

41. Fronto-orbital bristles conspicuous, well-developed, mostly reclinate or proclinate, or both (Figs. 28–32). Prescutellar acrostichal bristles present, well-developed (Fig. 49)....... .... HYDRELLIINAE....42

Fronto-orbital bristles either lateroclinate and inconspicuous, or lacking (Figs. 33–37). Prescutellar acrostichal bristles lacking .... PARYDRINAE, in part....51

42. Posterior notopleural bristle much farther from notopleural suture than anterior bristle (as in Fig. 46). Wing spotted (Figs. 51, 52) 43

Anterior and posterior notopleural bristles equidistant from notopleural suture (as in Fig. 45). Wing not spotted 44

43. R_{2+3} long, subparallel to C; second costal section over twice as long as third (Fig. 51) ... . ***Ilythea*** Haliday

3 spp.; widespread; Cresson 1944

R_{2+3} short, running almost straight to C; second costal section subequal to third (Fig. 52) .... ***Zeros*** Cresson

5 spp.; widespread; Cresson 1944

44. Eye with short dense hairs. Ocellar bristles seldom as strong as pseudopostocellar bristles, usually much weaker (Fig. 29). Postsutural supra-alar bristle usually short, not longer than posterior notopleural bristle (Fig. 49) .... ***Hydrellia*** Robineau-Desvoidy

57 spp.; widespread; Deonier 1971

Eye bare. Ocellar bristles stronger than the weak pseudopostocellar bristles (Figs. 30–32). Postsutural supra-alar bristle strong, longer than posterior notopleural bristle 45

45. Mid tibia without dorsal bristles. Shiny black species............... ***Typopsilopa*** Cresson

4 spp.; widespread; Wirth 1968

Mid tibia with one to four erect dorsal bristles. Dull species 46

46. C not extending to M, rarely extending beyond R_{4+5} (Fig. 53). Pedicel with strong dorsoapical spine (Figs. 30, 31) .... ***Notiphila*** Fallén....47

C extending to M. Pedicel with weak dorsoapical spine (Fig. 32)...................49

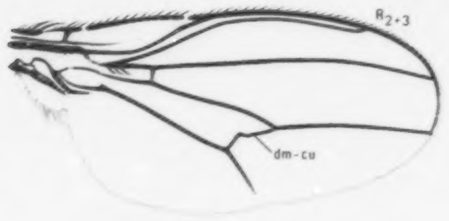
47. Facial bristles inserted close to parafacial; proclinate fronto-orbital bristles very strong (Fig. 30). Dark brown to black species .... ***Notiphila*** (***Dichaeta*** Meigen), in part

3 spp., the *caudata* group; widespread

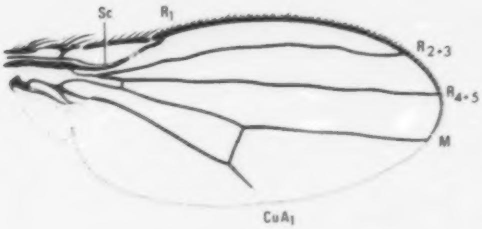
Facial bristles well-removed from parafacial; proclinate fronto-orbital bristles weak (Fig. 31). Ocherous to cinereous species 48

48. Mid tibia with four dorsal bristles. Facial bristles reduced, hair-like; two pairs of small proclinate fronto-orbital bristles present, lateral to larger reclinate bristle (Fig. 31). Mid femur of male lacking posteroventral comb of bristles ...***Notiphila*** (***Dichaeta*** Meigen), in part

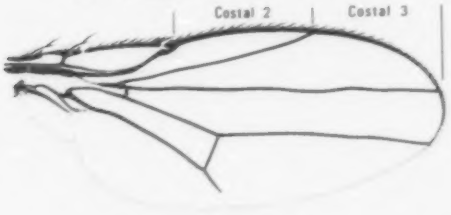
22 spp.; widespread; Mathis 1979*a*; see couplet 47



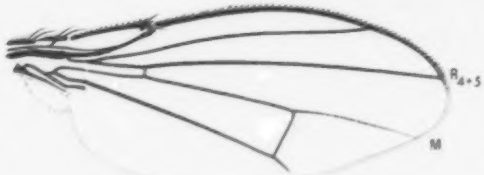
50 Clanoneurum americanum ♀



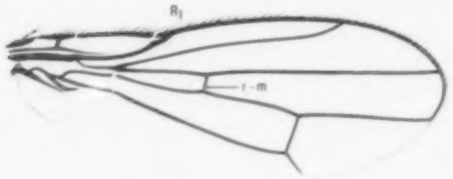
51 Ilythea spilota ♀



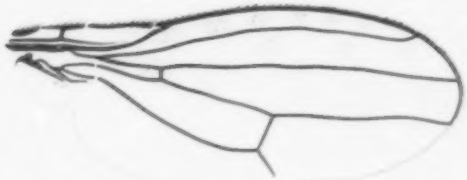
52 Zeros flavipes ♀



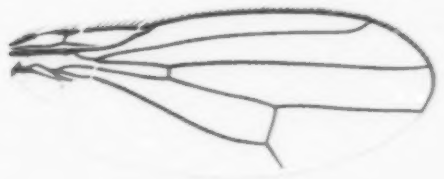
53 Notiphila (Dichaeta) aenigma ♂



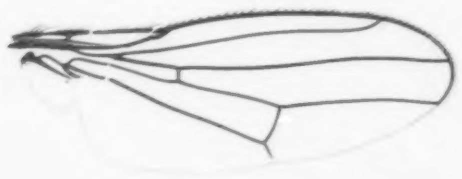
54 Parydra (Chaetoapnea) parasocia ♀



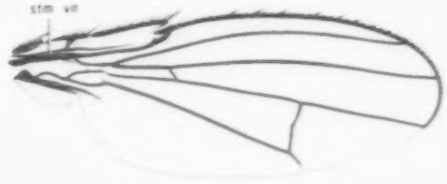
55 Callinapaea aldrichi ♂



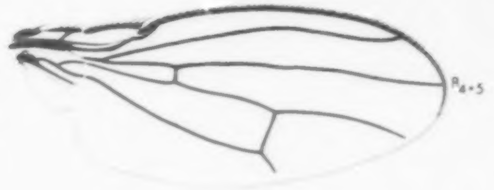
56 Eutaenionotum guttipennis ♂



57 Pelina truncatula ♂



58 Paracoenia bisetosa ♂



59 Scatophila cribrata ♂

Figs. 98.50–59. Wings: (50) *Clanoneurum americanum* Cresson; (51) *Ilythea spilota* (Curtis); (52) *Zeros flavipes* (Williston); (53) *Notiphila* (*Dichaeta*) *aenigma* Cresson; (54) *Parydra* (*Chaetoapnea*) *parasocia* Clausen; (55) *Callinapaea aldrichi* Sturtevant & Wheeler; (56) *Eutaenionotum guttipennis* (Stenhammar); (57) *Pelina truncatula* Loew; (58) *Paracoenia bisetosa* (Coquillett); (59) *Scatophila cribrata* (Stenhammar).

Abbreviation: stm vn, stem vein.

Mid tibia with three dorsal bristles. Facial bristles often stronger, bristle-like; usually one pair of small proclinate fronto-orbital bristles present lateral to larger reclinate bristle. Mid femur of male often with comb-like row of bristles along posteroventral margin .... ***Notiphila*** (***Notiphila*** Fallén)

25 spp.; widespread; Mathis 1979*a*

49. Small cinereous species, 2–2.5 mm long. Scutal setulae very few in number; katepisternal bristle absent .... ***Oedenops*** Becker

1 sp., *nudus* (Coquillett); southern, Neotropical

Larger dark species. Scutal setulae numerous; katepisternal bristle strong .... ***Paralimna*** Loew....50

50. Dark brown frequently shiny species, lacking cinereous coloration. Abdomen with or without olivaceous fasciae. Eye elongate. Gena narrow, at most one-fourth as high as eye (Fig. 32) .... ***Paralimna*** (***Phaiosterna*** Cresson)

2 spp.; southern and eastern U.S.A., Neotropical; Cresson 1946

Dull species, with some cinereous or ocherous markings, particularly on pleura. Abdomen with contrasting brown and cinereous fasciae. Eye round. Gena wide, at least three-sevenths as high as eye .... ***Paralimna*** (***Paralimna*** Loew)

3 spp.; widespread; Cresson 1946

51. Subcranial cavity large, gaping (Figs. 33, 34) 52

Subcranial cavity small to moderately large (Figs. 35–37) 56

52. Crossvein r-m located distinctly beyond junction of R_1 and C; second costal section 0.6–3.3 times as long as third (Fig. 54). Scutellum sometimes with apical tubercles or a median process or both .... ***Parydra*** Stenhammar....53

Crossvein r-m located directly below or slightly beyond junction of R_1 and C; second costal section 3.3–5.0 times as long as third (Figs. 55, 56). Scutellum without apical tubercles or a median process 54

53. Face convex in profile (Fig. 33) .... ***Parydra*** (***Parydra*** Stenhammar)

15 spp.; widespread; Clausen and Cook 1971

Face straight to concave in profile (Fig. 34) .... ***Parydra*** (***Chaetoapnaea*** Hendel)

16 spp.; widespread; Clausen and Cook 1971

54. Two strong fronto-orbital bristles present, each subequal to inner vertical bristle .... ***Rhinonapaea*** Wirth

1 sp., *metallica* (Cole); low Arctic

At most one strong fronto-orbital bristle present 55

55. One fronto-orbital bristle moderately strong, from a half to two-thirds as long as inner vertical bristle. Second costal section of wing 4.1–5.0 times as long as third section (Fig. 55) .... ***Callinapaea*** Sturtevant & Wheeler

2 spp.; widespread; Clausen and Cook 1971

All fronto-orbital bristles minute, at most one-sixth as long as inner vertical bristle. Second costal section of wing about 3.5 times as long as third section (Fig. 56) .... ***Eutaenionotum*** Oldenberg

1 sp., *guttipennis* (Stenhammar); northern

56. Posterior notopleural bristle much farther from notopleural suture than anterior bristle (as in Fig. 46) 57

Anterior notopleural bristle absent, or, if present, the two bristles equidistant from the notopleural suture (Fig. 47) 59

57. Face broad, concave, with prominent lower facial margin. Arista conspicuously pectinate; rays long (Fig. 35) .... ***Lemnaphila*** Cresson

1 sp., *scotlandae* Cresson; widespread

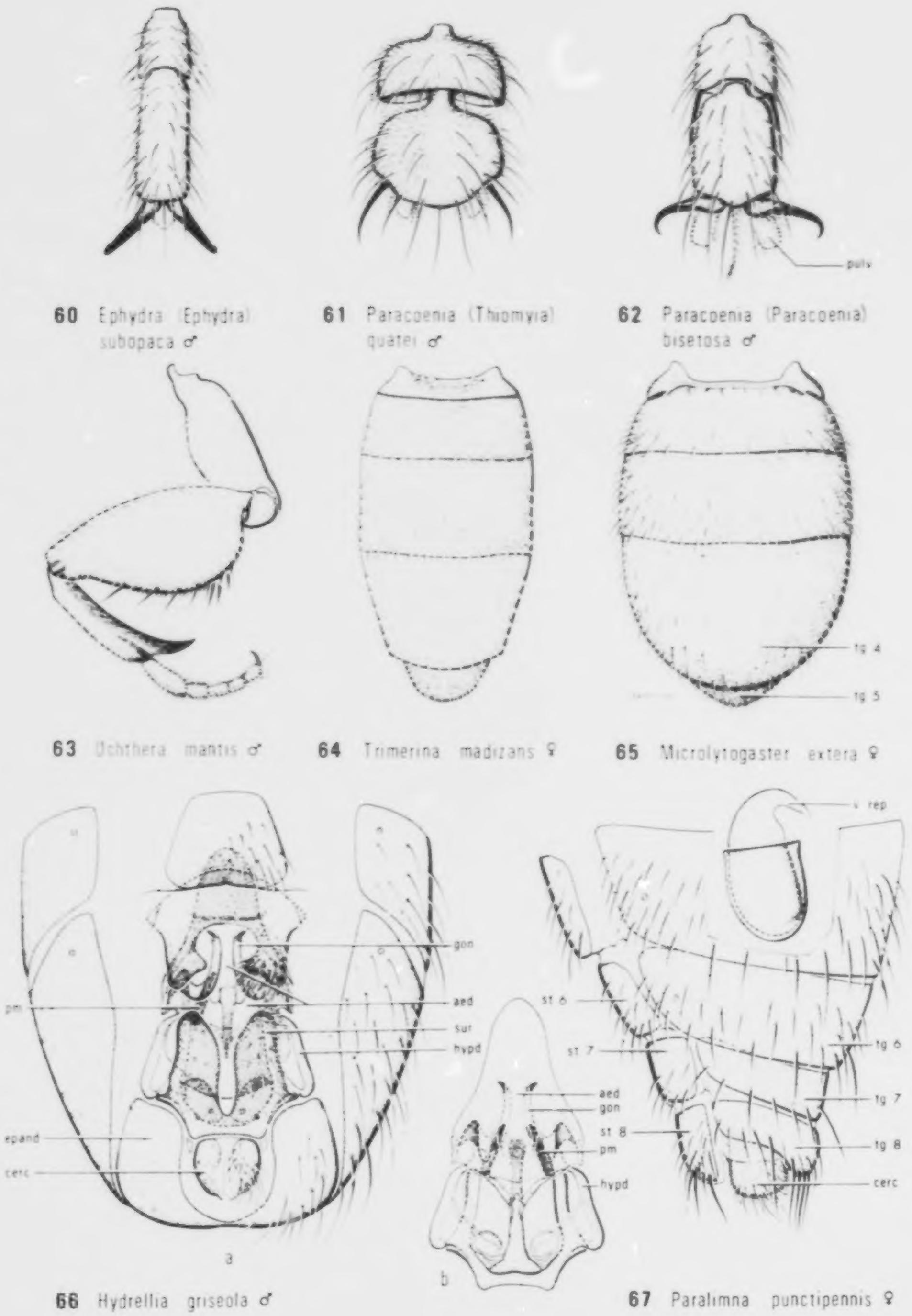
Face narrow, not concave; if face prominent, lower facial margin receding. Arista bare or haired (Fig. 36) 58

58. Arista bare or minutely haired (Fig. 36). Presutural dorsocentral bristle present .... ***Philygria*** Stenhammar

4 spp.; widespread; Sturtevant and Wheeler 1954 (as *Hydrina* Robineau-Desvoidy)

Arista short- to long-haired. Presutural dorsocentral bristle absent ...... ***Nostima*** Coquillett

8 spp.; widespread; Sturtevant and Wheeler 1954



60 Ephydra (Ephydra) subopaca ♂

61 Paracoenia (Thiomyia) quatei ♂

62 Paracoenia (Paracoenia) bisetosa ♂

63 Ochthera mantis ♂

64 Trimerina madizans ♀

65 Microlytogaster extera ♀

66 Hydrellia griseola ♂

67 Paralimna punctipennis ♀

Figs. 98.60–67. Tarsi, forelegs, abdomens, and terminalia: last two segments of fore tarsus of (60) *Ephydra* (*Ephydra*) *subopaca* Loew, (61) *Paracoenia* (*Thiomyia*) *quatei* (Wirth), and (62) *Paracoenia* (*Paracoenia*) *bisetosa* (Coquillett); (63) posterior view of left foreleg of *Ochthera mantis* (De Geer); dorsal views of abdomens of (64) *Trimerina madizans* (Fallén) and (65) *Microlytogaster extera* (Cresson); (66) male terminalia of *Hydrellia griseola* (Fallén); (67) female terminalia of *Paralimna punctipennis* (Wiedemann).

Abbreviations: aed, aedeagus; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; pulv, pulvillus; st, sternite; sur, surstylus; tg, tergite; v rep, ventral receptacle.

59. C extending at most slightly beyond R_{4+5} (as in Fig. 53). Tergite 4 at least three times as long as tergite 5 (Fig. 65) 60

C extending to M (Fig. 57). Tergite 4 at most twice as long as tergite 5 61

60. Abdominal tergites with lateral portions directed abruptly medioventrally and almost meeting on mid line so pleural membranes are almost hidden .... ***Axysta*** Haliday

2 spp.; widespread; Clausen 1983

Abdominal tergites with lateral portions curved smoothly downward, widely separated ventrally, and not hiding pleural membranes (Fig. 65) .... ***Microlytogaster*** Clausen

1 sp., *extera* (Cresson); widespread

61. Wing with R_{2+3} long; second costal section nearly three times as long as third (Fig. 57). Face flat or weakly carinate, not medially prominent. First flagellomere rounded at apex above (Fig. 42) .... ***Pelina*** Haliday

7 spp.; widespread; Clausen 1973

Wing with R_{2+3} short; second costal section less than twice as long as third. Face with low conical median prominence. First flagellomere usually angulate at apex above (Fig. 37) 62

62. Wing brown, with about 14 distinct white spots .... ***Pseudohyadina*** Clausen

1 sp., *longicornis* (Sturtevant & Wheeler); eastern

Wing unmarked or with at most faint spots or clouds at apex of R_1 and on crossveins 63

63. Tergite 4 longer, 1.3–2.0 times as long as tergite 5, both conspicuously punctate. Inner vertical bristle present; outer vertical bristle absent. Lateral margins of scutellum not densely pruinose, not appearing velvety. Length 2.04–3.20 mm .... ***Lytogaster*** Becker

8 spp.; widespread; Clausen 1982

Tergite 4 subequal in length to tergite 5, neither conspicuously punctate. Usually both vertical bristles present (Fig. 37), but if outer absent, then lateral margins of scutellum densely pruinose, appearing velvety. Length 1.45–2.30 mm .... ***Hyadina*** Haliday

9 spp.; widespread; Clausen 1983

64. Three or four pairs of postsutural dorsocentral bristles present, the three anterior pairs sometimes very short and weak. Disc of proepisternum with few to many fine setulae 65

Two pairs of postsutural dorsocentral bristles present, both pairs equally strong. Disc of proepisternum usually bare, sometimes with a few fine setulae 74

65. Prosternum setulose. Pulvilli much reduced or absent; tarsal claws long and nearly straight (Fig. 60) 66

Prosternum bare. Pulvilli well-developed; tarsal claws short and distinctly curved (Figs. 61, 62) 71

66. First flagellomere with a large bristle inserted laterally just below insertion of arista (Fig. 43) .... ***Setacera*** Cresson

8 spp.; widespread; Mathis 1982

First flagellomere without a lateral bristle 67

67. Three or four pairs of strong fronto-orbital bristles present (Figs. 1, 38). Anterior presutural intra-alar bristle present, subequal to posterior notopleural bristle .... ***Ephydra*** Fallén 68

Two pairs of strong fronto-orbital bristles present (Fig. 39). Anterior presutural intra-alar bristle either absent or much reduced, much smaller than posterior notopleural bristle ... 70

68. Two pairs of presutural dorsocentral bristles present, the anterior pair sometimes rather short. Face very thickly haired. Arista short, weakly haired, thicker on its basal half. Usually two posteriorly directed rows of well-developed cruciate interfrontal bristles present, with these rows closer to fronto-orbital bristles than to each other (Fig. 38). Tarsomere 1 of foreleg of male bearing ventral tuft of long hairs near tip ...... ***Ephydra*** (***Hydropyrus*** Cresson)

2 spp.; western North America; Wirth 1971

Only one pair of presutural dorsocentral bristles present (Fig. 1). Face with one strong row of facial bristles and one of oral bristles, otherwise thinly short-haired. Arista without markedly swollen basal region. Usually not more than one pair of interfrontal bristles situated as close to each other as to fronto-orbital bristles (Fig. 1). Tarsomere 1 of foreleg of male without ventral hair tuft 69

69. One pair of strong interfrontal bristles present (Fig. 1). Crossvein dm-cu making nearly a right angle with CuA_1 (Fig. 1). Palpus well-developed .... ***Ephydra*** **(*Ephydra*** Fallén)

13 spp.: widespread; Wirth 1971

Interfrontal bristles weak or absent. Crossvein dm-cu making an acute angle with CuA_1. Palpus small .... ***Ephydra*** **(*Halephydra*** Wirth)

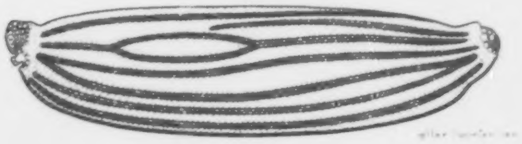
1 sp., *cinerea* Jones; widespread

70. Aristal rays short, at most half as long as width of pedicel; face sometimes with a cluster of strong bristles in middle (Fig. 39). Hind femur of male conspicuously swollen, with a short row of four or five stout bristles along anteroventral surface toward base; hind tibia of male with ventroapical tuft of hairs; hind tarsus of male variously modified .... ***Cirrula*** Cresson

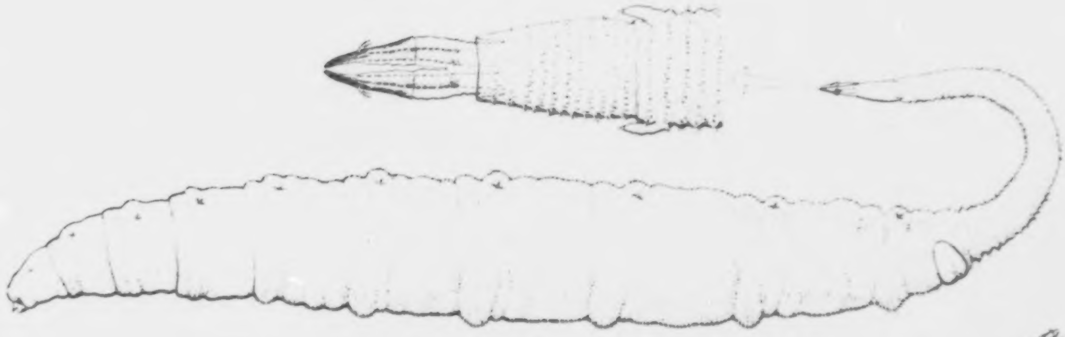
2 spp.: widespread, coastal; Mathis and Simpson 1981

Aristal rays long, subequal in length to width of pedicel; face without strong bristles in middle. Hind femur of male not differing markedly from mid or fore femur, lacking stout bristles as above; hind tibia of male lacking tuft of hairs; hind tarsus of male normal, cylindrical .... ***Dimecoenia*** Cresson

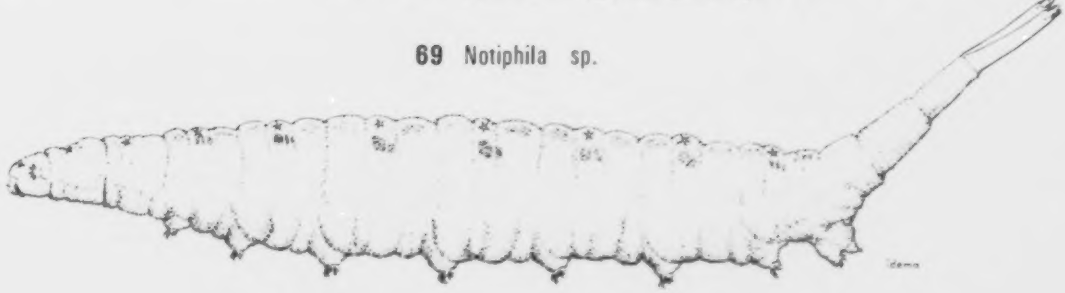
2 spp.: eastern, coastal; Mathis and Simpson 1981



68 Hydrellia bergi



69 Notiphila sp.



70 Ephydra sp.

Figs. 98.68–70. Egg and larvae: (68) egg of *Hydrellia bergi* Cresson; larvae in lateral view of (69) *Notiphila* sp., with enlargement of apex of respiratory tube, and (70) *Ephydra* sp.

71. One presutural and three postsutural dorsocentral bristles present. Postpronotal bristle absent or very short and weak, at most one-fourth as long as posterior notopleural bristle. Hind coxa bare posteriorly .... ***Coenia*** Robineau-Desvoidy

2 spp.; northern United States, Canada; Mathis 1975

One presutural and four postsutural dorsocentral bristles present. Postpronotal bristle distinct, weak or strong, at least one-half as long as posterior notopleural bristle. Hind coxa bare or with a row of setae posteriorly 72

72. Stem vein with one or two setulae above, inserted beyond transverse septum (Fig. 58). Scutellum with dorsum convex. Hind coxa with row of setae posteriorly along ventral margin .... ***Paracoenia*** Cresson 73

Stem vein bare above. Scutellum with dorsum almost flat. Hind coxa bare posteriorly along ventral margin .... ***Calocoenia*** Mathis

2 spp.; northern and western; Mathis 1975

73. Tarsi short and broad, with dense pubescence; tarsal claws extremely slender (Fig. 61) .... ***Paracoenia*** (***Thiomyia*** Wirth)

1 sp., *quatei* (Wirth); southern California

Tarsi normal, not short and broad, lacking dense pubescence; tarsal claws well-developed (Fig. 62) .... ***Paracoenia*** (***Paracoenia*** Cresson)

6 spp.; widespread; Mathis 1975

74. C extending to or just beyond apex of R_{4+5} (Fig. 59) .... ***Scatophila*** Becker

22 spp.; widespread; Sturtevant and Wheeler 1954

C extending to apex of M 75

75. Arista pectinate above (Fig. 44) .... ***Philotelma*** Becker

1 sp., *alaskense* Cresson; northern

Arista bare to macropubescent 76

76. Only one pair of lateroclinate fronto-orbital bristles present. Wing with very distinct pattern of many irregular pale and dark spots .... ***Limnellia*** Malloch

11 spp.; widespread; Mathis 1978

Two or three pairs of lateroclinate fronto-orbital bristles present. Wing with pattern of small pale spots or unmarked 77

77. Gena usually with a distinct bristle much longer and stronger than other genal hairs, but if without a distinct bristle, then presutural dorsocentral bristle absent. Wing with distinct to very obscure pale spots .... ***Scatella*** Robineau-Desvoidy 78

Gena without bristle, with a series of uniform fine hairs. Presutural dorsocentral bristle present. Wing without pale spots .... ***Lamproscatella*** Hendel 80

78. Presutural dorsocentral bristle absent; one pair of strong acrostichal bristles present at suture .... ***Scatella*** (***Scatella*** Robineau-Desvoidy), in part

12 spp.; widespread; Sturtevant and Wheeler 1954

Presutural dorsocentral bristle present, strong; one pair of strong acrostichal bristles present or absent at suture 79

79. Only one pair of strong acrostichal bristles present, inserted at suture .... ***Scatella*** (***Neoscatella*** Malloch)

3 spp.; widespread; Sturtevant and Wheeler 1954

Acrostichal bristles generally weak, short, continuing in a postsutural row to base of scutellum .... ***Scatella*** (***Scatella*** Robineau-Desvoidy), in part

3 spp., the *triseta* group; western; Mathis and Shewell 1978

80. Posterior notopleural bristle much farther from notopleural suture than anterior bristle (Fig. 46). Eye longer than high, generally oriented at slightly oblique angle to lower margin of gena .... ***Lamproscatella*** (***Haloscatella*** Mathis)

5 spp.; widespread but mostly western; Mathis 1979*b*

Anterior and posterior notopleural bristles equidistant from notopleural suture (as in Fig. 45). Eye slightly higher than long, appearing round 81

81. Posterior fronto-orbital bristle closer to inner vertical bristle than to anterior fronto-orbital bristle. Gena at least 0.35 times as high as eye. Frontal vitta shiny .... ***Lamproscatella*** (***Thinoscatella*** Mathis)

2 spp.; western and northern, coastal; Mathis 1979*b*

Posterior fronto-orbital bristle closer to anterior fronto-orbital bristle than to inner vertical bristle. Gena at most 0.25 times as high as eye. Frontal vitta at most subshiny .... ***Lamproscatella*** (***Lamproscatella*** Hendel)

4 spp.; western and northern; Mathis 1979*b*

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CHLOROPIDAE

99

Curtis W. Sabrosky

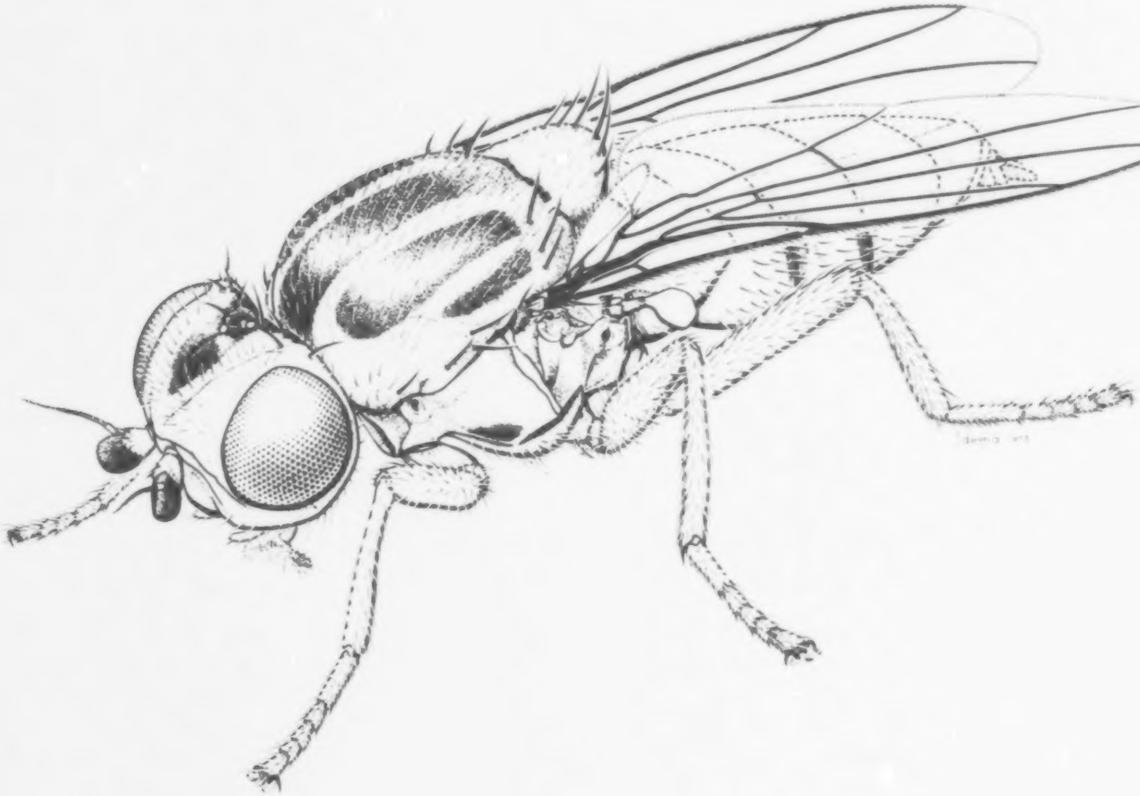

Fig. 99.1. Female of *Chlorops certimus* Adams.

Small flies 1.5–5.0 mm long, rarely larger, with reduced bristling (Fig. 1). Ocellar (=frontal) triangle characteristically well-developed. Propleuron anteriorly with sharp carina. Wing venation reduced; C with only subcostal break; $A_1 + CuA_2$ and cell cu*p* absent; CuA_1 commonly with a distinct flexure opposite or before midlength of cell bm + dm (Fig. 36).

Adult. Head: frons broad in both sexes, usually with a large, strongly sclerotized, plate-like, sharply margined ocellar triangle (Figs. 1–19); surface of ocellar triangle varying from smooth and polished to densely pruinose and dull, usually with a single row of piliferous punctures on or just outside its lateral margins, occasionally with two or more rows on each side of triangle, rarely entirely punctate. Head profile usually showing frons only slightly projecting, face receding or slightly concave, and vibrissal angle obtusely rounded (rarely projecting and acutely angulate). Eye large, round or ovate in outline, with long axis usually vertical or nearly so except in genera with projecting frons, bare to short-haired, rarely densely long-haired. Face flat or with low carina; carina well-developed though narrow in a few genera, rarely broad and flat (*Lipara* Meigen). Antenna (Figs. 20–30) porrect; flagellomere 1 commonly orbicular or nearly so, sometimes reniform, occasionally elongate; arista micropubescent to short pubescent, rarely entirely bare, sometimes long-haired, sometimes flattened and ensiform. Bristles of head reduced, usually weak, seldom strong; inner and outer vertical, postocellar, and ocellar bristles commonly present; postocellar bristles parallel to convergent or cruciate; fronto-orbital bristles usually consisting of a row of short reclinate hairs, but occasionally consisting of one to several pairs of strong and distinct bristles that are usually erect and reclinate (rarely proclinate, *Apotropina* Hendel); vibrissa often present, but usually weak, hair-like, and inconspicuous.

Thorax: scutum usually longer than broad (Figs. 53–55), convex, finely haired with hairs often set in definite rows, and sometimes with coarse distinct piliferous punctures; scutellum (Figs. 44–52) short and rounded to elongate conical, sometimes with marginal tubercles bearing bristles. Propleuron sharply carinate anteriorly (Fig. 4.166). Thoracic bristling greatly reduced, rarely with bristles on disc of scutum; one postpronotal bristle (often weak and inconspicuous), one anterior and one or two posterior notopleural bristles, and one postalar, one posterior dorsocentral, and one propleural bristle (often pale, weak, and inconspicuous) almost always present; one pair of apical scutellar and one or two (rarely more) pairs of subapical scutellar bristles present. Upper half of pleuron usually glabrous; anepisternum occasionally with hairs. Legs (Figs. 56–64) usually short and slender, without bristles; mid or hind tibia sometimes with a curved apical or subapical spur (Figs. 56–59, 63); commonly in Oscinellinae and some Chloropinae, hind tibia posterodorsally with an elongate oval slightly depressed tibial organ (Figs. 60, 61), long known in Chloropidae as a sensory area (renamed by Andersson 1977), but this organ possibly is secretory in function like a similar area in some Sepsidae. Wing (Figs. 31–43) rarely absent or reduced, usually hyaline, rarely with any color pattern; venation remarkably consistent throughout family; C continuing at most to M_{1+2}, with subcostal break; Sc usually very faint, present as a trace close to R_1, evanescent distally; R_{4+5} and M_{1+2} usually long, ending respectively before and behind apex of wing; cells bm and dm wholly confluent, appearing as one long cell; CuA_1 commonly with a distinct flexure in its long penultimate sector, opposite or before middle of cell bm + dm; crossveins r-m and dm-cu usually present, although crossvein dm-cu (posterior crossvein) absent in a few species; A_1 and cell cu*p* always absent; anal area of wing usually well-developed and broadly rounded, seldom narrowed (*Stenoscinis* Malloch, Fig. 33).

Abdomen: broad, tapering to apex, with segments preceding terminalia usually approximately equal in length; spiracles of tergites 1–5 situated in membrane adjacent to lateral edges of tergites. Male terminalia (Figs. 65–66), surveyed by Griffiths (1972) and Andersson (1977), showing extreme variation in position of spiracles, symmetry, and development and fusion of parts so that familial generalizations are difficult; epandrium (tergite 9) well-developed, with movable surstyli; cerci usually small, separate, or fused at bases, or completely fused; aedeagus greatly reduced. Female terminalia (Fig. 67) simple; cerci usually evident as a pair of long-haired pendant lobes that are rarely fused to form a compressed and knife-like (*Sacatonia* Sabrosky) or spike-like (*Opetiophora* Loew) ovipositor; two sclerotized spermathecae present, rudimentary, attached to long and very fine ducts that are "rolled into a single heavy spool-like coil" in Oscinellinae but not in Chloropinae, at least in the species sampled (Sturtevant 1925–1926).

Larva. Those of stem miners studied most thoroughly, described as slender, elongate, cylindrical, and tapering anteriorly (Figs. 68–71); those of gall formers not as slender. Zones of tiny spines present on ventral surface or as bands encircling segments. Anterior spiracles (Fig. 69) somewhat fan-shaped, usually with four to nine papillae, although up to 17 described for some species. Posterior spiracles (Figs. 71, 72) borne on ends of short cylindrical processes that are typically parallel or only slightly divergent and project distinctly from surface of larva (and puparium); three short oval spiracular slits present on each spiracular plate; plates each bearing simple to long-branched interspiracular hairs.

The immature stages of Chloropidae are little known in North America, although several identical or congeneric species have been investigated in Europe. Hennig (1952) listed several of these references, and Balachowsky and Mesnil (1935) figured larvae and puparia and recorded damage caused by several pests of cereals.

Biology and behavior. Larvae of Chloropidae have varied food habits. Many are phytophagous, some damaging cereals and other grasses. These include the destructive frit fly *Oscinella frit* (Linnaeus), stem maggots, notably the wheat stem maggot, *Meromyza americana* Fitch, and the gout fly of wheat and barley in Europe, *Chlorops pumilionis* (Bjerkander). Others are saprophagous, feeding in the frass left by other insects, on decaying leaf sheaths, or on decaying vegetable matter in the soil. A few species have been bred from fungi. A few are gall formers, such as *Lipara lucens* Meigen of Europe, which produces large terminal galls on the giant reed *Phragmites*. Some are predacious. Larvae of *Thaumatomyia glabra* (Meigen) are important predators on the sugarbeet root aphid, *Pemphigus populivenae* Fitch, and larvae of *Pseudogaurax* Malloch feed on eggs in a wide variety of egg masses, such as those of spiders (Araneida), tussock moths (Lymantriidae), and mantids (Mantidae). A few are known as inquilines, but their precise food habit is not clear. One of the most unusual habits is that of species of the Australian genus *Batrachomyia* Krefft, whose larvae live under the skin on the backs of frogs.

Adult chloropids, sometimes called grass flies, are often abundant and are commonly collected by sweeping grass, sedges, and other low vegetation. Some frequent flowers, and some annoy man and animals by hovering about eyes or ears or by feeding at external body openings, wounds, and sores (the eye gnats and yaws flies of the Western Hemisphere, or the eye fly of the Orient).

Classification and distribution. The family occurs in all faunal regions and at present consists of approximately 2000 described species, classified in three subfamilies, Siphonellopsinae, Oscinellinae, and Chloropinae, containing over 160 genera; 55 genera and about 270 described species are known from the Nearctic region. Many undescribed species are known, especially in tropical regions. Becker (1912) published, as the last in a series of monographs that encompassed the entire world, a treatment of the Chloropidae of the Nearctic region, but his keys are in most cases far out-of-date. Later generic keys exist for the various faunal regions (especially see Andersson 1977). Those for the Palaearctic region are particularly helpful in North America because most of our genera are Holarctic. The species and genera of America north of Mexico were cataloged by Sabrosky (1965). New genera and new generic combinations have been published by Sabrosky (1980*b*). One fossil species, *Protoscinella electrica* Hennig from Baltic amber, is known (Hennig 1965).

Key to genera

1. Wing absent, or brachypterous with indeterminate venation (recognized as Chloropidae by large ocellar triangle, carinate propleuron, and reduced bristling) .... ***Conioscinella*** Duda, in part

1 sp., unnamed; Manitoba, Ontario, Quebec, Massachusetts, Ohio

Wing well-developed; venation evident 2

2. C extending to M_1 (Figs. 31–39), except in *Dicraeus ingratus* (Loew) in which it ends midway between apices of R_{4+5} and M_1. Tibial organ usually present posterodorsally on hind tibia (as in Figs. 60, 61). Most species with entirely or predominantly black body 3

C extending to R_{4+5} or barely beyond (Figs. 40–43). Tibial organ usually absent on hind tibia. Most species yellow or reddish, with red to black stripes ..... CHLOROPINAE 45

3. Fronto-orbital bristles long and proclinate, with upper one sometimes lateroclinate; ocellar bristles proclinate and divergent. Postpronotum with two long strong bristles; inner one directed medially, and outer one posteriorly ..... SIPHONELLOPSINAE .... ***Apotropina*** Hendel

8 spp.; widespread; Sabrosky 1951*b*, 1980*a* (=*Lasiopleura* Becker).

Fronto-orbital bristles usually short, weak, and hair-like, always erect and reclinate; ocellar bristles erect and convergent to cruciate, rarely proclinate. Postpronotum without a strong medially directed bristle except in densely bristled *Eugaurax* and *Chaetochlorops*; posteriorly directed bristle commonly weak and appressed .... OSCINELLINAE 4

4. Hind tibia with a curved apical or preapical spur located ventrally or slightly anteroventrally (Figs. 56–59); spur generally long and strong, in a few species fairly short but equal in length to diameter of tibia, except in *Opetiophora* where length of spur is less than diameter of tibia and height of gena nearly twice as wide as first flagellomere 5

Hind tibia without a strong spur; if a short spur present, length shorter than diameter of tibia and gena much narrower than described for *Opetiophora*, or two pairs of well-developed fronto-orbital bristles present 10

5. Scutellum trapezoidal in outline; apical scutellar bristles widely separated and on small tubercles at outer angles (Fig. 44). Arista ensiform, broad and flat, located at apex of dorsally produced first flagellomere (as in Fig. 20). One anterior and one posterior notopleural bristle present .... ***Ceratobarys*** Coquillett

1 sp., *eulophus* (Loew); southeastern U.S.A.

Scutellum rounded apically or elongate conical; apical scutellar bristles not so widely separated nor borne on tubercles, although sockets may be enlarged. Arista slender, short or long pubescent, with first flagellomere suborbicular to reniform. Usually one anterior and two posterior notopleural bristles present 6

6. First flagellomere reniform, much broader than long, bulged dorsally between base of segment and base of arista (Fig. 21). Scutellum flattened dorsally, elongate conical, as long as broad (Fig. 45). Hind tibial spur apical, almost as long as first tarsomere (Fig. 56) .... ***Cadrema*** Walker

1 sp., *pallida* (Loew); southern Florida, Neotropical

First flagellomere orbicular, at most as long as broad; arista located near base of segment. Scutellum not conical, broadly rounded distally. Hind tibial spur not as previously described, commonly preapical, but if apical then strongly curved (Fig. 57) 7

7. Gena broad, nearly twice as wide as first flagellomere (Fig. 24). Postpronotal bristle strong, as well-developed as notopleural bristles. Female with terminalia forming a shining black spike-like ovipositor .... ***Opetiophora*** Loew

1 sp., *straminea* Loew; west central U.S.A. south to Mexico

Gena narrower, at most as wide as first flagellomere. Postpronotal bristle weak, obviously less developed than notopleural bristles. Ovipositor not as in *Opetiophora*; cerci of usual form, each a dull long-haired pendant appendage 8

8. Thorax almost entirely, and ocellar triangle entirely, polished black. Frons and gena shining but not polished, and not pruinose .... ***Liohippelates*** Duda

10 spp.; widespread from southern Canada south to Neotropical region; Sabrosky 1941*b* (*pusio* group)

Thorax entirely or chiefly finely pruinose, at least with large and conspicuous spot of gray or brownish gray pruinescence before and below wing base, covering most of notopleuron, anepisternum, and anepimeron. Ocellar triangle polished or dull; frons and gena dull, more or less pruinose 9

9. Facial carina well-developed but thin, separating distinct antennal grooves; lower marginal portion of face warped forward, and vibrissal angle at least slightly forwardly produced anterior to eye; face concave in profile; ocellar bristles well-separated, erect and parallel or slightly convergent .... ***Hippelates*** Loew, in part

6 spp.; widespread in southern Canada and U.S.A.; Sabrosky 1941*b* (*plebejus* group)

Facial carina at most weakly indicated on upper face, not distinctly separating antennal grooves; face not concave in profile; lower marginal portion of face not warped forward and vibrissal angle not produced anterior to eye; ocellar bristles relatively close together, erect and cruciate, at least at tips .... ***Apallates*** Sabrosky, in part

10 spp.; widespread from Quebec south to Neotropical region; Sabrosky 1940 (in part), 1941*b* (*dissidens* group), 1980*b*

10. R_{2+3} extremely short and cell r_1 narrow; second costal sector much shorter than third sector (Fig. 32) .... ***Siphunculina*** Rondani

1 sp., *striolata* (Wiedemann); southern Florida, Neotropical

R_{2+3} not exceptionally short; second costal sector usually subequal to or longer than third sector, but if second sector short, R_{2+3} concave anteriorly and cell r_1 not narrow 11

11. Facial carina high, broad, flat, widely separating deep antennal grooves. Head, scutum, and much of abdomen densely covered with closely appressed yellow hairs. Body length 6.0–8.0 mm, unusually large for a chloropid .... ***Lipara*** Meigen

1 sp., *lucens* Meigen; Connecticut (immigrant, possibly established)

Carina sometimes absent, or present as a low ridge or narrow knife-like partition between antennal grooves, or if rarely broadened then other characters do not apply. Hairs normal, black, rarely pale, not densely and closely appressed. Body length 1.5–2.5 mm, much smaller species 12

12. Postocellar bristles stout, straight, and parallel or slightly divergent. Eye bare or with minute sparse pubescence. Gena rather broad, divided diagonally into a rough and shining posteroventral half (or more) and a smooth and silvery pruinose anterodorsal portion that is continuous with whitish lower half of face 13

Postocellar bristles usually convergent to cruciate, but if rarely parallel then eye densely pubescent or gena not as previously described 14

13. Postpronotum, notopleuron, scutum posteriorly, and scutellum studded with numerous extra bristles (Fig. 54) .... ***Chaetochlorops*** Malloch

1 sp., *inquilinus* (Coquillett); eastern half of U.S.A.

Bristling normal, with only one postpronotal bristle, one anterior notopleural bristle, and one or two posterior notopleural bristles present .... ***Fiebrigella*** Duda

3 spp.; widespread in U.S.A.; Sabrosky 1970 (as *Goniopsita* Duda)

14. Notopleuron, scutum posteriorly, and scutellum studded with numerous extra bristles. Yellow species, often with scutum striped .... ***Eugaurax*** Malloch

1 sp., *floridensis* Sabrosky; eastern; Sabrosky 1950*c*

Bristling normal, with only one anterior and one or two posterior notopleural, one postalar, one posterior dorsocentral, one pair of apical scutellar, and usually one or two pairs of subapical scutellar bristles present. Most species black 15

15. Ocellar triangle only, or both triangle and scutum highly shining, entirely or predominantly without pruinescence; if triangle entirely pruinose (rarely), then hind tibia with a short anteroventral spur, or frons with two pairs of fronto-orbital bristles developed; ocellar triangle usually smooth and shiny but this shine sometimes interrupted by piliferous punctures or fine striations or shagreening[1] 16

Ocellar triangle, scutum, and scutellum dull, densely gray pruinose, sometimes subshining if only thinly pruinose; three small polished spots rarely present on ocellar triangle adjacent to ocelli 36

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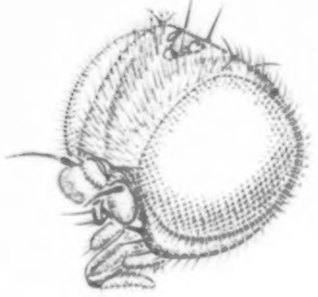
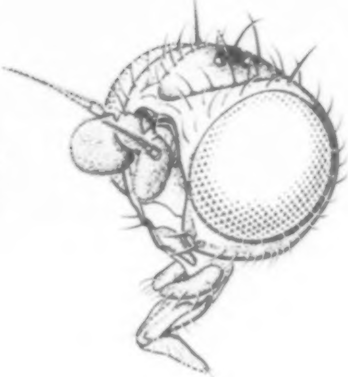
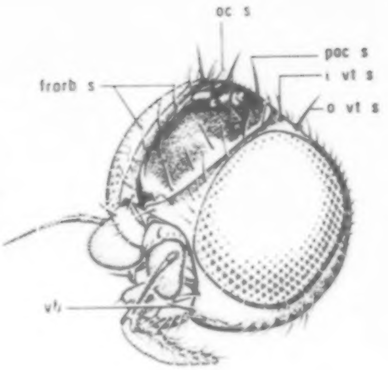
[1] *Olcella punctifrons* (Becker), a tiny yellow species with three linear black stripes on scutum, is keyed to couplet 36 although the large round shining black spot in the middle of the ocellar triangle might suggest the opposite choice.



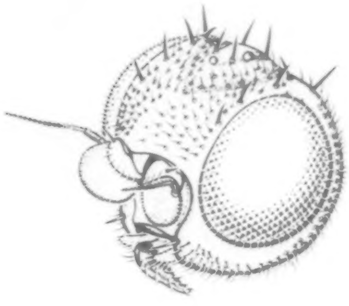
2 Calamoncosis minima ♂



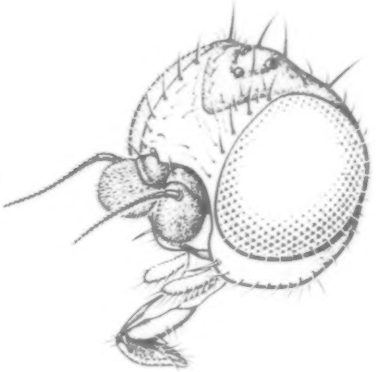
3 Oscinella frit ♀



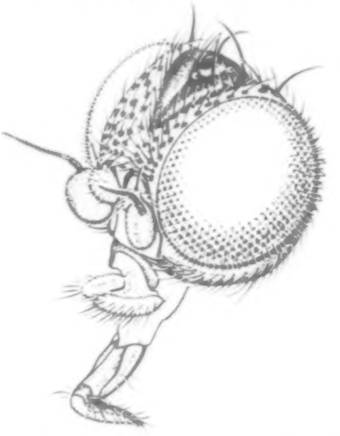
4 Hapleginella conicola ♀



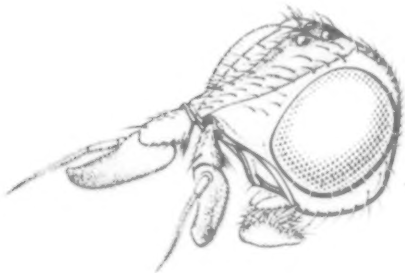
5 Aphanotrigonum scabrum ♂



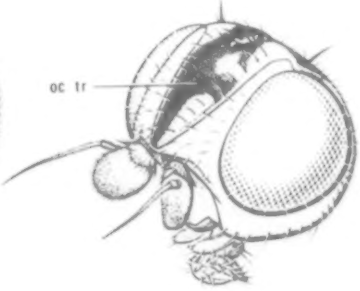
6 Incertella incerta ♀



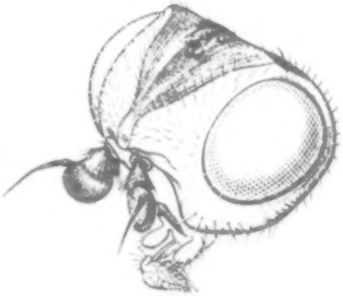
7 Speccafrons mallochi ♂



8 Ectecephala albistylum ♂



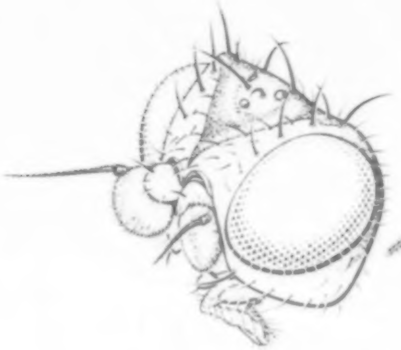
9 Thaumatomyia glabra ♂



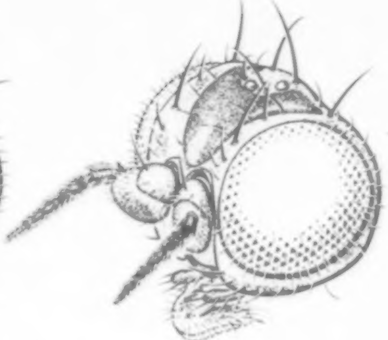
10 Epichlorops exilis ♀

Figs. 99.2–10. Heads: (2) *Calamoncosis minima* (Strobl) (not Nearctic); (3) *Oscinella frit* (Linnaeus); (4) *Hapleginella conicola* (Greene); (5) *Aphanotrigonum scabrum* (Aldrich); (6) *Incertella incerta* (Becker); (7) *Speccafrons mallochi* (Sabrosky); (8) *Ectecephala albistylum* Macquart; (9) *Thaumatomyia glabra* (Meigen); (10) *Epichlorops exilis* (Coquillett) (*continued*).

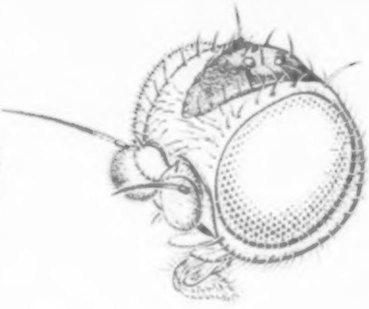
Abbreviations: frorb s, fronto-orbital bristle; i vt s, inner vertical bristle; oc s, ocellar bristle; oc tr, ocellar triangle; o vt s, outer vertical bristle; poc s, postocellar bristle; vb, vibrissa.



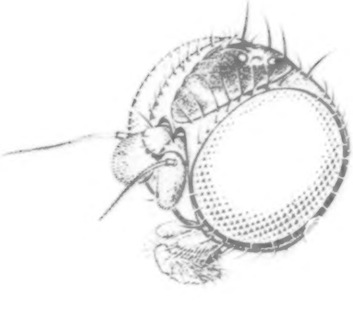
11 Pseudopachychaeta approximatonervis ♂



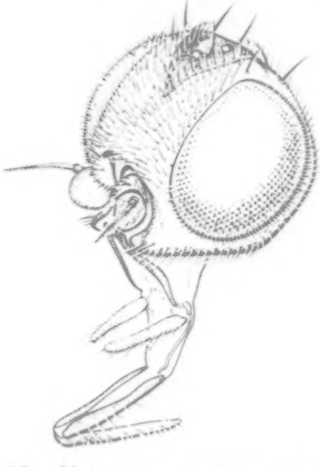
♂ **12** Monochaetoscinella nigricornis ♂



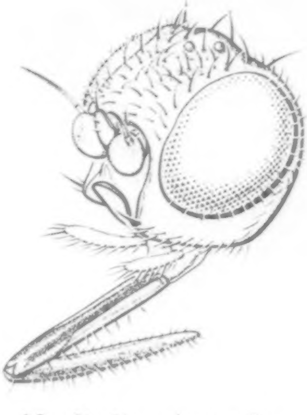
13 Oscinisoma alienum ♀



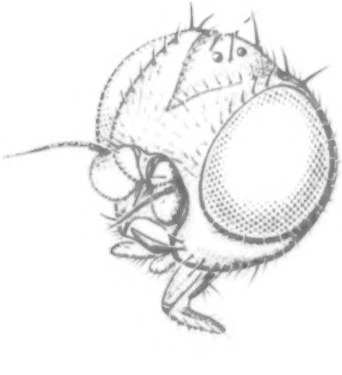
14 Stenoscinis longipes ♂



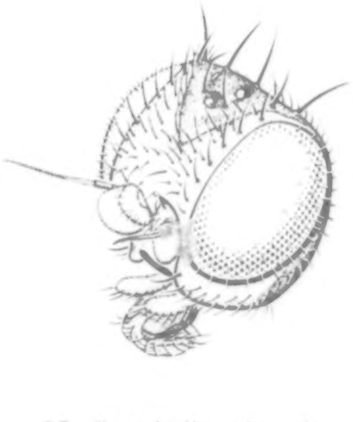
15 Siphonella oscinina ♀



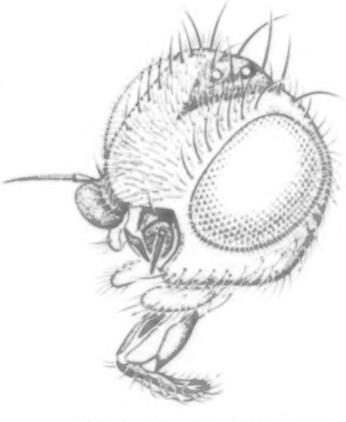
16 Olcella cinerea ♀



17 Malloewia nigripalpis ♂



18 Neoscinella gigas ♀



19 Dasyopa latifrons ♂

Figs. 99.11–19. Heads (*concluded*): (11) *Pseudopachychaeta approximatonervis* (Zetterstedt); (12) *Monochaetoscinella nigricornis* (Loew); (13) *Oscinisoma alienum* (Becker); (14) *Stenoscinis longipes* (Loew); (15) *Siphonella oscinina* (Fallén); (16) *Olcella cinerea* (Loew); (17) *Malloewia nigripalpis* (Malloch); (18) *Neoscinella gigas* (Sabrosky); (19) *Dasyopa latifrons* (Loew) .

16. Anepisternum long-haired, with polished black surface; thorax shining black, without pruinescence. In Nearctic species ultimate section of M_{1+2} anteriorly convex near base, thence continuing straight to wing margin (Fig. 37) .... ***Rhodesiella*** Adams

1 sp., *brimleyi* Sabrosky; southeastern U.S.A.

Anepisternum usually bare of hairs, rarely with a few hairs dorsally, with or without pale pruinescence; thorax shining or dull. Ultimate section of M_{1+2} straight from anterior distal corner of cell bm-dm to apex of wing, rarely gently convex anteriorly over entire length 17

17. Ocellar triangle with two or more rows of coarse piliferous punctures on each side (Fig. 2) .... ***Calamoncosis*** Enderlein

1 sp., unnamed; Michigan

Ocellar triangle at most with only one row of usually fine, piliferous punctures on each side, with punctures sometimes only on basal half 18

18. Ocellar bristles strong, proclinate, widely divergent. Second costal section unusually long, 2.5–3.0 times as long as third section; anal area of wing well-developed ..... ***Psilacrum*** Becker

1 sp., *arpidia* (Malloch); eastern North America; Malloch 1918 (key to varieties as *Oscinoides* Malloch)

Not with this combination of characters 19

19. Frons with a single pair of strong fronto-orbital bristles located anterior to middle of frons and flanking a long ocellar triangle (Fig. 12) .... ***Monochaetoscinella*** Duda

2 spp.; southeastern U.S.A.; Sabrosky 1948

Frons with two or three pairs of fronto-orbital bristles or bristle-like hairs, or with all fronto-orbital bristles hair-like and numerous 20

20. One anterior and one long and strong posterior notopleural bristle present; in some species an upper posterior bristle weakly developed but still appearing as if only one strong bristle present (in doubtful cases, e.g. *Oscinisoma*, scutellum flattened and rugose, with marginal scutellar bristles borne on tubercles) 21

One anterior and two strong posterior notopleural bristles present (in an aberrant *Oscinella* sp. there is no anterior bristle, and just one posterior bristle present, but then scutellum not flattened nor rugose) 27

21. Scutellum flattened, rugose, blunt apically, more or less trapezoidal in outline, with disc as long as or longer than broad; marginal scutellar bristles, especially apical ones, borne on distinct large or small tubercles (Fig. 46); typically two pairs of subapical scutellar bristles present 22

Scutellum broadly rounded apically, much broader than long (Fig. 48); marginal scutellar bristles not borne on tubercles; apical bristles usually widely separated; one pair of subapical bristles present 23

22. First flagellomere reniform, extended dorsally; arista flattened, typically broad and sword-shaped but sometimes narrow (Fig. 20); if arista exceptionally slender (two atypical species), then first flagellomere still reniform and two pairs of strong fronto-orbital bristles also present .... ***Elachiptera*** Macquart

17 spp.; widespread in North America from Alaska southward; Sabrosky 1948

First flagellomere shorter than broad but not extended dorsally, not strongly reniform (Fig. 13); arista slender, not flattened nor thickened. Fronto-orbital bristles short, rather uniform .... ***Oscinisoma*** Lioy

1 sp., *alienum* (Becker); eastern half of U.S.A., southeastern Canada

23. Arista flattened or thickened, densely long-haired, inserted at anterodorsal angle of subquadrate first flagellomere (Fig. 26) .... ***Melanochaeta*** Bezzi

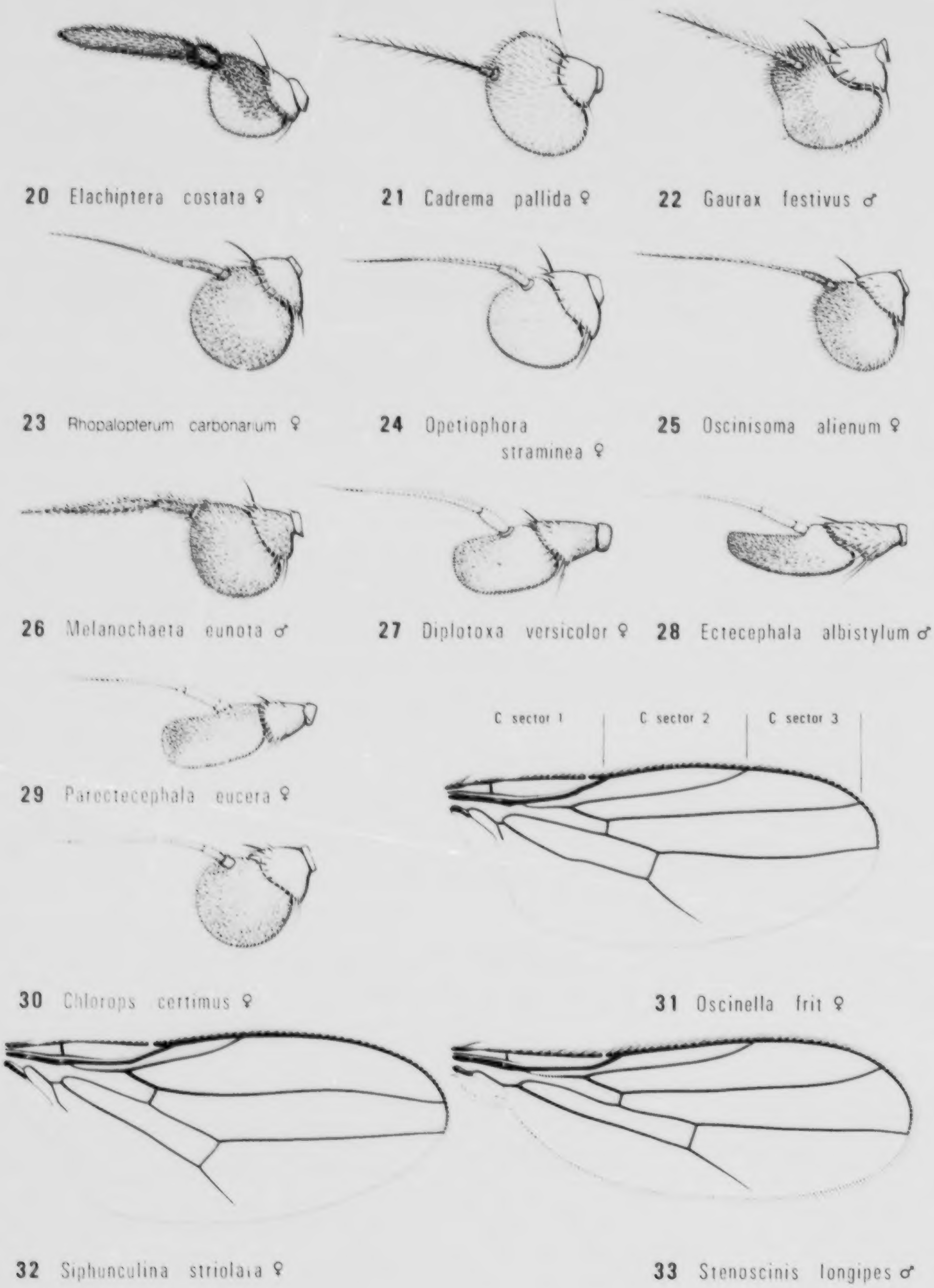
3 spp.; widespread from Alberta to Quebec south through U.S.A.; Sabrosky 1948

Arista not often densely haired, but if so then not thickened, always inserted near base of reniform first flagellomere 24

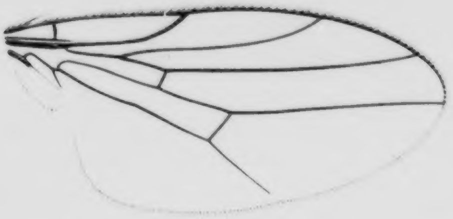
24. Anal area of wing narrow, without anal angle (Fig. 33); cell c exceptionally long and narrow, narrower than width of cell br and 10–12 times as long as wide (length measured from humeral crossvein to juncture of R_1 and C). Ocellar and postocellar bristles proclinate; ocellar bristles divergent. Body narrow and wing elongate .... ***Stenoscinis*** Malloch

2 spp.; southeastern Canada south through U.S.A.; Sabrosky 1961

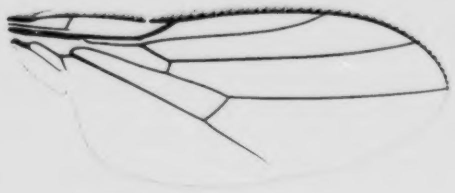
Anal area of wing broader, with rounded anal angle (Fig. 34); cell c in most genera fairly short and broad, as wide as or wider than width of cell br (Fig. 34). Ocellar and postocellar bristles erect, cruciate or convergent. Usually body stocky and wing short and broad 25


20 Elachiptera costata ♀
21 Cadrema pallida ♀
22 Gaurax festivus ♂
23 Rhopalopterum carbonarium ♀
24 Opetiophora straminea ♀
25 Oscinisoma alienum ♀
26 Melanochaeta eunota ♂
27 Diplotoxa versicolor ♀
28 Ectecephala albistylum ♂
29 Parectecephala eucera ♀
C sector 1
C sector 2
C sector 3
30 Chlorops certimus ♀
31 Oscinella frit ♀
32 Siphunculina striolata ♀
33 Stenoscinis longipes ♂

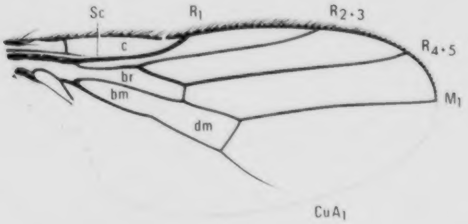
Figs. 99.20–33. Left antennae, left lateral views, and wings: antennae of (20) *Elachiptera costata* (Loew), (21) *Cadrema pallida* (Loew), (22) *Gaurax festivus* Loew, (23) *Rhopalopterum carbonarium* (Loew), (24) *Opetiophora straminea* Loew, (25) *Oscinisoma alienum* (Becker), (26) *Melanochaeta eunota* (Loew), (27) *Diplotoxa versicolor* (Loew), (28) *Ectecephala albistylum* Macquart, (29) *Parectecephala eucera* (Loew), and (30) *Chlorops certimus* Adams; wings of (31) *Oscinella frit* (Linnaeus), (32) *Siphunculina striolata* (Wiedemann), and (33) *Stenoscinis longipes* (Loew) (*continued*).



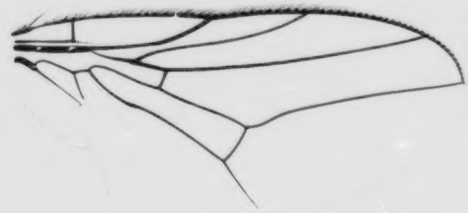
34 Gaurax festivus ♂



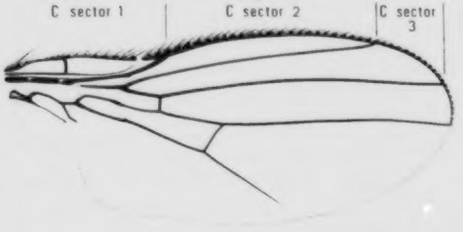
35 Hapleginella conicola ♀



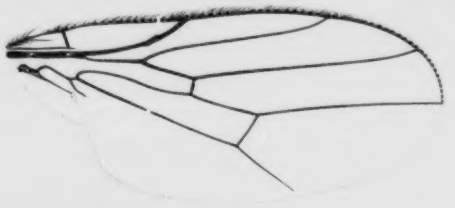
36 Neoscinella gigas ♀



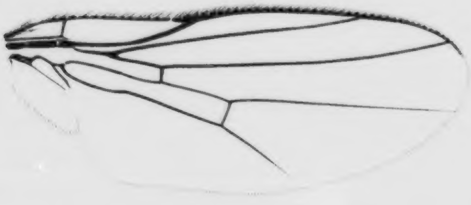
37 Rhodesiella brimleyi ♀



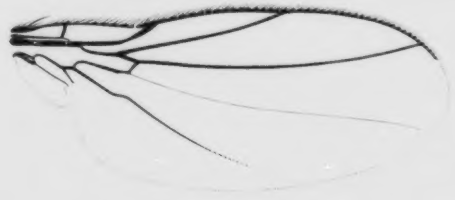
38 Dicraeus incongruus ♂



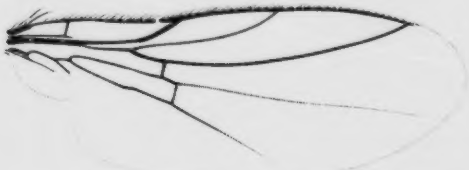
39 Aphanotrigonum scabrum ♂



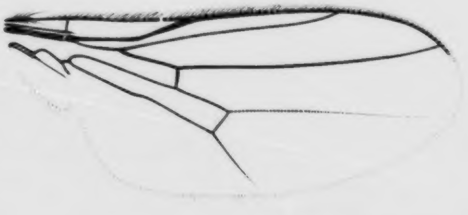
40 Chlorops certimus ♀



41 Elliponeura debilis ♂



42 Diplotoxa versicolor ♀



43 Trigonomma fossulatum ♂

Figs. 99.34–43. Wings (*concluded*): (34) *Gaurax festivus* Loew; (35) *Hapleginella conicola* (Greene); (36) *Neoscinella gigas* (Sabrosky); (37) *Rhodesiella brimleyi* Sabrosky; (38) *Dicraeus incongruus* Aldrich; (39) *Aphanotrigonum scabrum* (Aldrich); (40) *Chlorops certimus* Adams; (41) *Elliponeura debilis* Loew; (42) *Diplotoxa versicolor* (Loew); (43) *Trigonomma fossulatum* (Loew).

25. Cell r_1 short and broad, opposite the end of R_1 much broader than cell r_{2+3}; R_{2+3} decidedly concave anteriorly (Fig. 34). Cell c unusually broad, approximately twice width of distal portion of cell br. Sc not evident, its path shown by a long pale streak from base of curved distal section of R_1 to subcostal break; R_1 of approximately uniform width throughout its length .... ***Gaurax*** Loew, in part

24 spp.; chiefly eastern North America; Sabrosky 1951*a*

Cell r_1 narrower, not obviously wider than cell r_{2+3} and usually narrower; R_{2+3} in most species longer and not so decidedly concave (Fig. 31). Cell c narrower, often barely wider than width of distal portion of cell br. Sc fused with R_1 along nearly full length of latter; in most species distal portion of R_1 thickened and angulate at point where short streak of Sc extends to subcostal break 26

26. Fronto-orbital bristles hair-like and uniform in length, or lengthening slightly from front to rear. Eye sparsely and microscopically pubescent .... ***Rhopalopterum*** Duda

10 spp.; widespread in North America south from Alaska; Sabrosky 1936 (in part), 1961 (in part), 1980*b*

Two, occasionally three, outstanding pairs of fronto-orbital bristles present. Eye densely pubescent .... ***Biorbitella*** Sabrosky

4 spp.; western North America; Sabrosky 1980*b* (see footnote to couplet 41)

27. Scutellum elongate conical, with long straight apical scutellar bristles approximated at bases and diverging apically (Fig. 47); thorax shining yellow with black pattern on scutum or on scutellum or both .... ***Pseudogaurax*** Malloch

3 spp.; southern U.S.A.; Sabrosky 1966

Scutellum short, not as in *Pseudogaurax*, but if somewhat elongate then apical scutellar bristles not approximated at bases and usually convergent to cruciate, or vibrissal angle projecting and facial profile concave; thorax usually black 28

28. Scutellum strongly narrowed apically, subconical, as long as broad at base. Vibrissal angle acutely angulate, strongly produced snout-like beyond anterior margin of frons (Fig. 15). Eye densely long-haired. Postocellar bristles parallel. Scutum densely and evenly punctate; acrostichal and dorsocentral rows as such not evident .... ***Siphonella*** Macquart

1 sp., *oscinina* (Fallén); Holarctic, widespread in U.S.A. and Canada

Scutellum broadly rounded, obviously shorter than broad at base. Vibrissal angle slightly or not at all produced (as in Fig. 17), and then not snout-like as shown for *Siphonella* (Fig. 15). Eye in most species only sparsely beset with minute or short hairs. Postocellar bristles convergent or cruciate. Scutum rarely densely punctate; acrostichal and dorsocentral rows of punctures usually evident and usually with distinct spaces between them 29

29. Cell r_1 short and broad, opposite the end of R_1 much broader than cell r_{2+3}; R_{2+3} decidedly concave anteriorly (Fig. 34); cell c unusually broad, approximately twice as wide as distal portion of cell br .... ***Gaurax*** Loew, in part

see couplet 25; atypical spp.

Cell r_1 not obviously broader than cell r_{2+3} and usually narrower; R_{2+3} in most species longer and not so decidedly concave (Fig. 31); cell c narrower, often barely wider than width of distal portion of cell br 30

30. Head in profile (Fig. 17) concave anteriorly, with vibrissal angle less than 90°, and projecting in front of anterior margin of eye (except in *M. abdominalis* (Becker) whose abdomen is entirely yellow); facial carina strong and complete, extending to lower marginal portion of face .... ***Malloewia*** Sabrosky

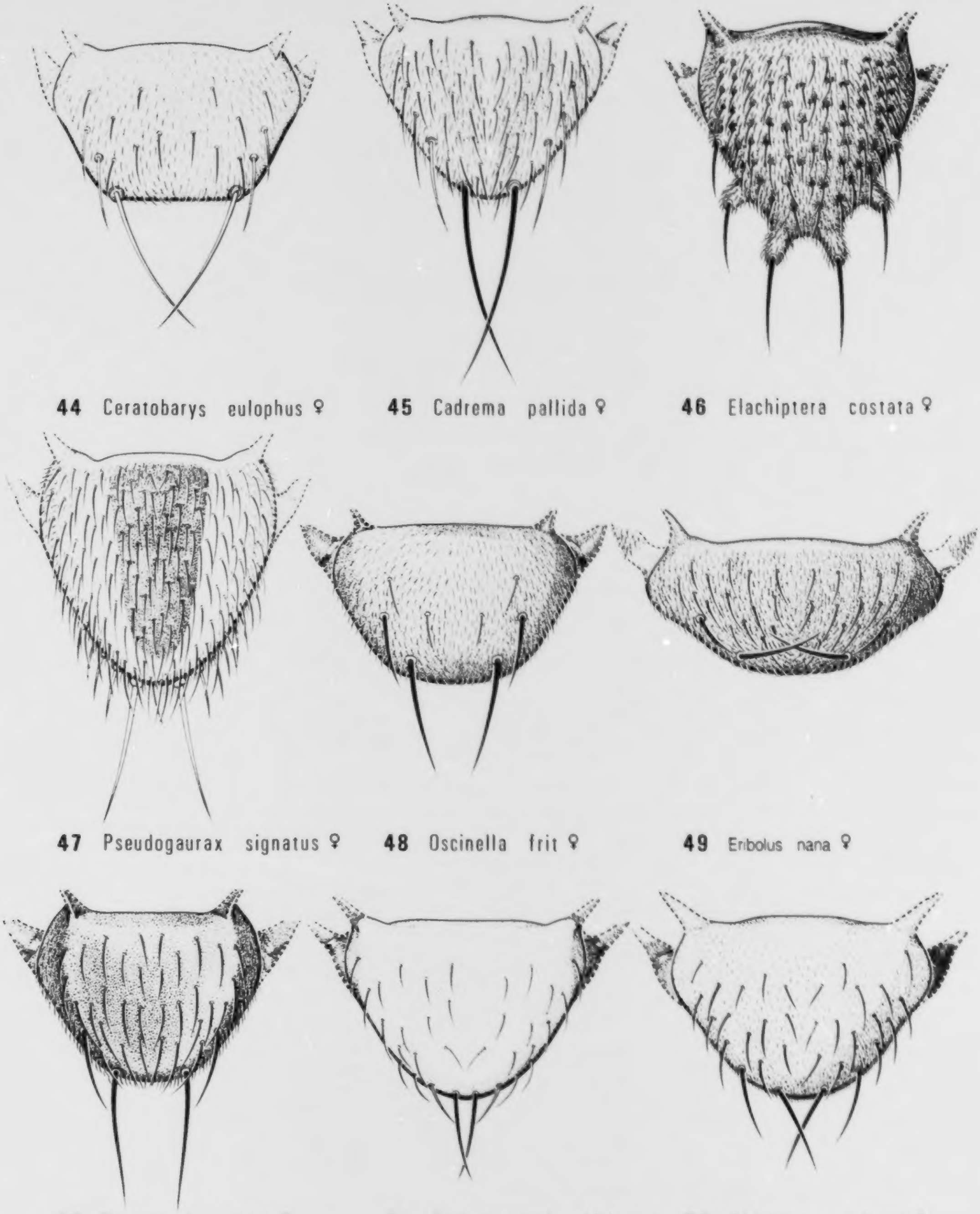
8 spp.; widespread in southern Canada and U.S.A.; Sabrosky 1936 (*Madiza* in part), 1980*b*

Head in profile not or very slightly concave, with vibrissal angle approximately 90° and not projecting in front of eye (Fig. 7); facial carina usually incomplete below 31

31. Eye densely pubescent. Frons outside ocellar triangle with distinctive speckled pattern; hairs arising from bare shining spots evenly distributed in finely gray pruinose field (Fig. 7). Male terminalia with enlarged semiglobose surstyli .... ***Speccafrons*** Sabrosky

1 sp., *mallochi* (Sabrosky); eastern half of U.S.A.; Sabrosky 1980*b*

Eye bare or sparsely beset with minute hairs. Frons with smooth and uniform surface whether shining or pruinose. Male terminalia with surstyli either slender and tapering or broadly flattened 32



44 Ceratobarys eulophus ♀ **45** Cadrema pallida ♀ **46** Elachiptera costata ♀

47 Pseudogaurax signatus ♀ **48** Oscinella frit ♀ **49** Eribolus nana ♀

50 Neoscinella gigas ♀ **51** Thaumatomyia glabra ♂ **52** Chlorops certimus ♀

Figs. 99.44–52. Scutellums, dorsal view: (44) *Ceratobarys eulophus* (Loew); (45) *Cadrema pallida* (Loew); (46) *Elachiptera costata* (Loew); (47) *Pseudogaurax signatus* (Loew); (48) *Oscinella frit* (Linnaeus); (49) *Eribolus nana* (Zetterstedt); (50) *Neoscinella gigas* (Sabrosky); (51) *Thaumatomyia glabra* (Meigen); (52) *Chlorops certimus* Adams.

32. Hind tibia anteroventrally with short bristle-like spur, one-half as long as, or at most equal in length to, diameter of tibial apex (Fig. 59). Scutum highly convex 33

Hind tibia without a spur; if rarely with a tiny spur (*Oscinella grandissima* Sabrosky), scutum flattened and broadened 34

33. Ocellar bristles recurved, subparallel or convergent. Head and thorax chiefly polished black; thorax pruinose around wing base .... ***Lioscinella*** Duda

Neotropical

Ocellar bristles erect or slightly proclinate, not at all recurved, typically cruciate. Head and thorax pruinose, at least in part; thorax pruinose at least on scutellum and with a large lateral spot on each side covering notopleuron and most of anepisternum and anepimeron .... ***Apallates*** Sabrosky, in part

3 spp.; widespread in U.S.A.; Sabrosky 1940 in part, 1980*b*; see couplet 9

34. Scutum and scutellum sparsely beset with fine, scarcely noticeable, piliferous punctures; scutellum short and broadly rounded, convex and smooth dorsally, and sparsely haired (two to four hairs); apical scutellar bristles widely separated; on each side a weak and hair-like subapical bristle arising nearly midway to base of scutellum (Fig. 48) .... ***Oscinella*** Becker

3 spp.; widespread in North America; Sabrosky 1936, in part

Scutum and scutellum with numerous more or less coarse piliferous punctures, usually densely set and at least obviously punctate; scutellum broadly rounded to subconical, usually more or less flattened and rugose dorsally; apical scutellar bristles closer together; subapical scutellar bristles on each side usually bristle-like, though short, and closely approximated to an apical bristle (as in Fig. 50); sometimes a second lateral scutellar bristle present proximal to subapical bristle 35

35. Cell br obviously though slightly broadened near middle, with sides of cell not parallel distally, obviously narrowing from midpoint to crossvein r-m (Fig. 35). Ocellar triangle long, extending to, or almost to, anterior margin of frons; a row of interfrontal hairs present along each side of full length of ocellar triangle, typically situated distinctly toward middle from edge of triangle (Fig. 4) .... ***Hapleginella*** Duda

1 sp., *conicola* (Greene); widespread in southern Canada and northern U.S.A.

Cell br not broadened near middle, with sides of cell parallel in distal half (Fig. 36). Ocellar triangle short, usually half to two-thirds length of frons, with interfrontal hairs situated on extreme edges of triangle; anterior rows of hairs often diverging from triangle .... ***Neoscinella*** Sabrosky

3 spp.; northern half of U.S.A. and southeastern Canada; Sabrosky 1980*b*

36. Scutum with three deeply incised lines of coarse punctures, a median acrostichal line and two usually doubled outer dorsocentral lines; similar but less strongly marked intra-alar lines also present above wing bases (Fig. 53) .... ***Tricimba*** Lioy[2]

7 spp.; widespread in southern Canada and U.S.A.; Sabrosky 1938

Scutum without deeply incised lines of punctures, although often with slightly depressed lines of finer punctures in median acrostichal and dorsocentral positions. In doubtful cases proboscis slender, elongate, and geniculate, with slender sclerotized labella 37

37. R_{2+3} and second costal sector (between apices of R_1 and R_{2+3}) exceptionally long; second sector 2.8–3.4 times as long as third sector (Fig. 38). Gena at least moderately broad, shining, microscopically striate. Epandrium in male large, knob-like, with long and often conspicuously exposed surstyli .... ***Dicraeus*** Loew

6 spp.; widespread in North America; Sabrosky 1950*b*

R_{2+3} and second costal sector much shorter; second sector usually barely longer than third sector, but rarely as much as 2.5 times longer than third sector and then differing in other characters. Gena usually dull, pruinose. Epandrium in male rather small and inconspicuous 38

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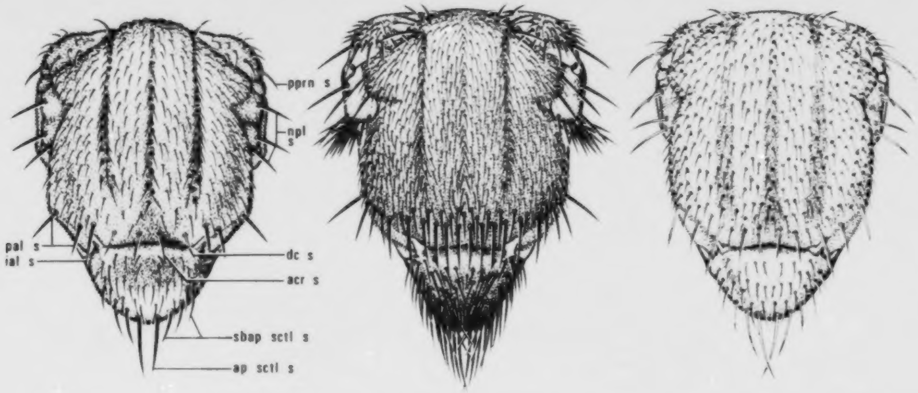
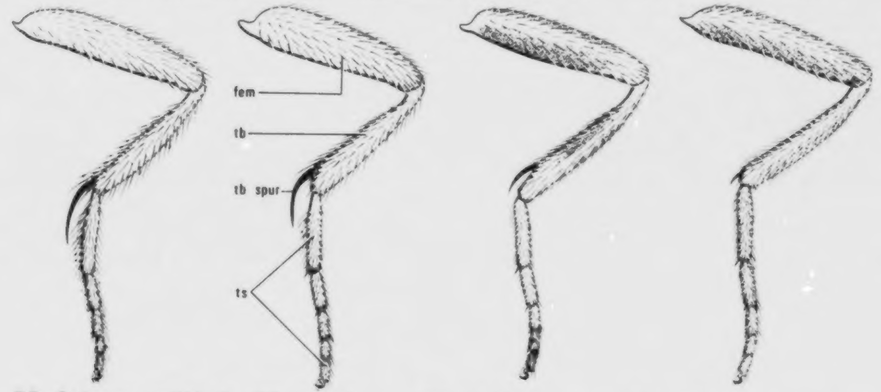
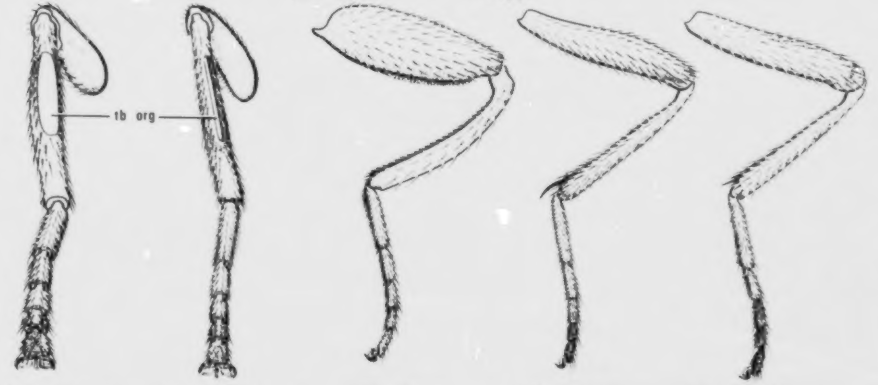
[2] *Oscinella melancholica* Becker, now referred to *Tricimba*, is atypical in having the scutal lines only slightly incised. The proboscis is short, labella broad and fleshy, and scutellum flattened with apical bristles approximated and two pairs of short subapical bristles close to apical bristles on distal half of scutellum.



53 Tricimba trisulcata ♀ **54** Chaetochlorops inquilinus ♂ **55** Olcella cinerea ♀



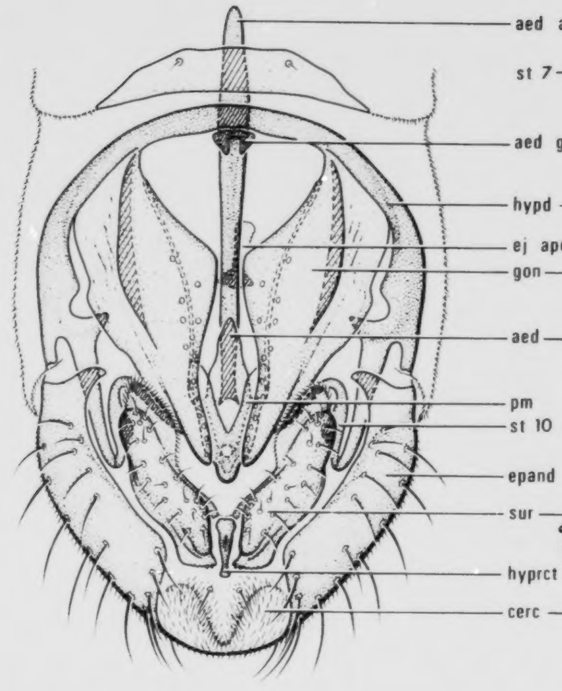
56 Cadrema pallida ♀ **57** Hippelates plebejus ♂ **58** Liohippelates bishoppi ♀ **59** Apallates coxendix ♀



60 Thaumatomyia glabra ♂ **61** Cetema subvittatum ♀ **62** Meromyza americana ♀ **63** Cetema subvittatum ♀ **64** Epichlorops exilis ♀

Figs. 99.53–64. Thoraces and legs: dorsal views of thoraces of (53) *Tricimba trisulcata* (Adams), (54) *Chaetochlorops inquilinus* (Coquillett), and (55) *Olcella cinerea* (Loew); left hindleg of (56) *Cadrema pallida* (Loew), (57) *Hippelates plebejus* Loew, (58) *Liohippelates bishoppi* (Sabrosky), (59) *Apallates coxendix* (Fitch), (60) *Thaumatomyia glabra* (Meigen), (61) *Cetema subvittatum* (Loew), and (62) *Meromyza americana* Fitch; midleg of (63) *Cetema subvittatum* (Loew) and (64) *Epichlorops exilis* (Coquillett).

Abbreviations: acr s, acrostichal bristle; ap sctl s, apical scutellar bristle; dc s, dorsocentral bristle; fem, femur; ial s, intra-alar bristle; npl s, notopleural bristle; pal s, postalar bristle; pprn s, postpronotal bristle; sbap sctl s, subapical scutellar bristle; tb, tibia; tb org, tibial organ; ts, tarsus.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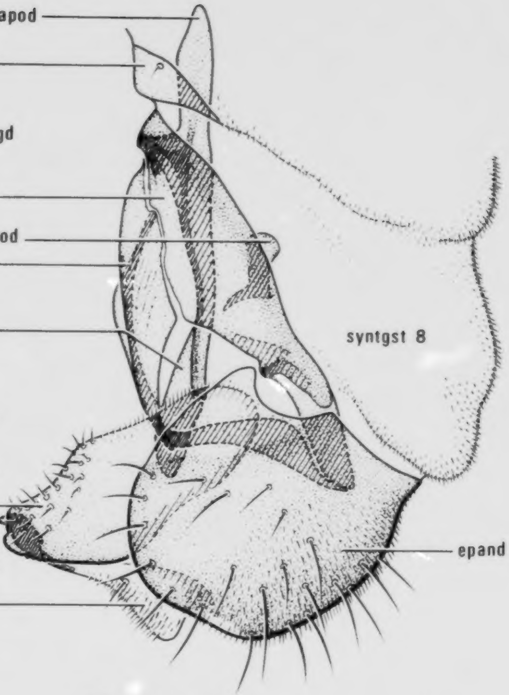
65 Chlorops rubicundus ♂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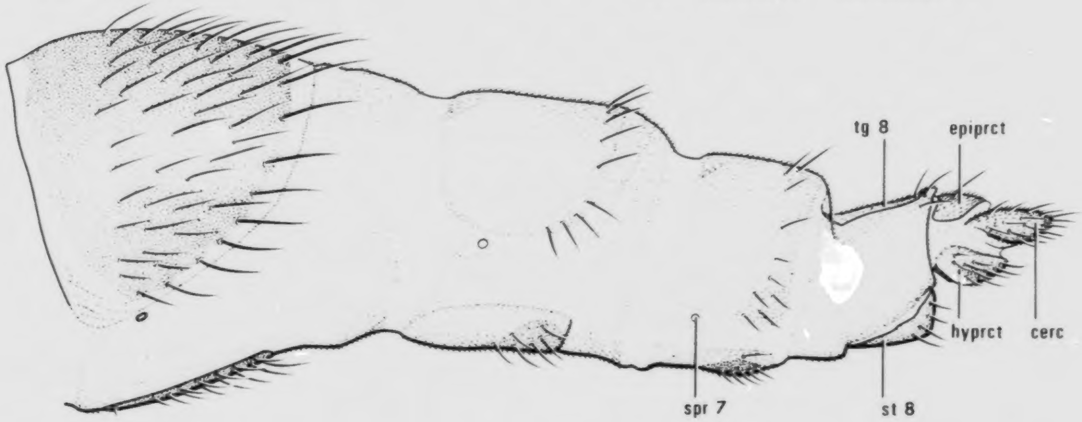
66 Chlorops rubicundus ♂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67 Chlorops rubicundus ♀

Figs. 99.65–67. Terminalia: (65) ventral view and (66) lateral view of male terminalia of *Chlorops rubicundus* Adams; (67) lateral view of female terminalia of *Chlorops rubicundus*.

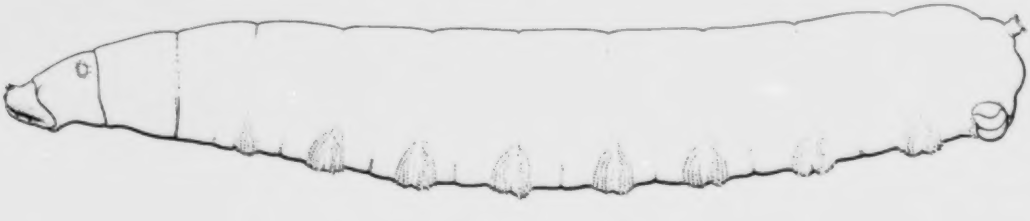
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

38. Ocellar triangle with two rows of coarse piliferous punctures on each side (Fig. 5). R_{2+3} and R_{4+5} strongly diverging at base; R_{2+3} bisinuate; cell r_{2+3} twice as wide as cell r_1 opposite end of R_1 (Fig. 39). Scutum short, broader than long .... ***Aphanotrigonum*** Duda
2 spp.; north from California to Alaska and east to Connecticut; Sabrosky 1936

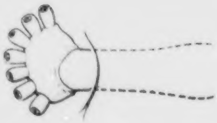
Ocellar triangle with only one row of piliferous punctures on each side. R_{2+3} and R_{4+5} usually diverging at a more sharply acute angle; R_{2+3} nearly straight basally, either straight on entire length or curving toward C and slightly to greatly concave anteriorly; cell r_{2+3} at most not so strongly broadened. Scutum usually as long as, or longer than, broad 39

39. One anterior and one posterior notopleural bristle present 40

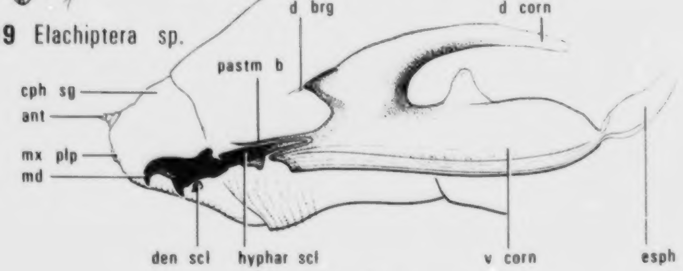
One anterior and two posterior notopleural bristles present 42



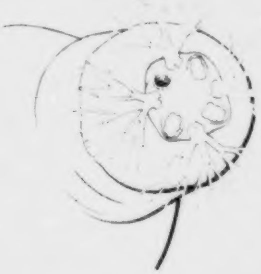
68 Elachiptera sp.



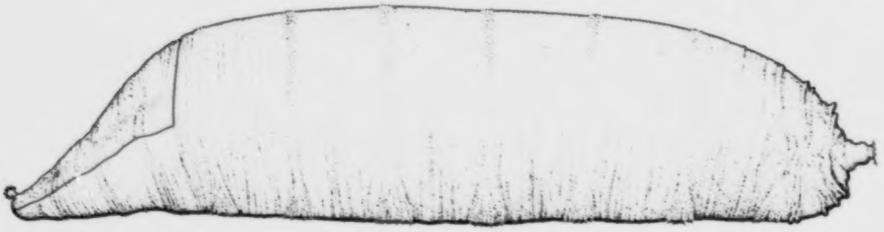
69 Elachiptera sp.



70 Elachiptera sp.



71 Elachiptera sp.



72 Elachiptera sp.

Figs. 99.68–72. Immature stages of *Elachiptera* sp.: (68) entire larva; (69) anterior spiracle of larva; (70) larval head and cephalopharyngeal skeleton; (71) posterior larval spiracle; (72) puparium.

Abbreviations: ant, antenna; cph sg, cephalic segment; d brg, dorsal bridge; d corn, dorsal cornu; den scl, dental sclerite; esph, esophagus; hyphar scl, hypopharyngeal sclerite; md, mandible; mx plp, maxillary palpus; pastm b, parastomal bar; v corn, ventral cornu.

40. Scutum flattened in profile, especially so on posterior slope; thorax longer than high .... ***Eribolus*** Becker

4 spp.; widespread in North America; Sabrosky 1950*a*

Scutum convex; thorax higher than long 41

41. Height of gena greater than width of first flagellomere; facial carina well-developed though narrow and knife-like, forming a narrow partition between distinct antennal grooves. Ovipositor compressed knife-like ..... ***Sacatonia*** Sabrosky

1 sp., *graminivora* Sabrosky; New Mexico, Colorado; Sabrosky 1967

Height of gena obviously much less than, usually about half, width of first flagellomere; facial carina a low ridge above, flattening out below. Ovipositor not compressed knife-like... ..... ***Incertella*** Sabrosky[3]

7 spp.; widespread in North America; Sabrosky 1936, 1980*b*

42. Hind tibia with a short anteroventral spur, shorter than tibial diameter (as in Fig. 59)..... ..... ***Hippelates*** Loew, in part

see couplet 9; atypical undescribed spp.

Hind tibia without a spur 43

43. Facial carina strong and extending in full height to lower marginal portion of face and visible in profile (Fig. 16), or vibrissal angle strongly produced and face concave in profile or both; vibrissal angle distinctly projecting in front of anterior margin of eye, as viewed in profile (Fig. 19). Proboscis typically elongate and geniculate; both prementum and labella slender, well-sclerotized 44

Facial carina at most a low ridge, or if slightly developed not visible in profile; face typically receding as seen in profile, with vibrissal angle not produced but forming a 90° angle or greater; vibrissal angle even with or behind anterior margin of eye, atypically slightly in front of eye. Proboscis short; labella more or less fleshy, or at least not elongate .... ***Conioscinella*** Duda, in part

5 spp.; widespread in North America; Sabrosky 1936; see couplet 1

44. Scutum with one median acrostichal line and, in each dorsocentral position, one to three dense lines of coarse piliferous punctures, with characteristically divergent hairs (Fig. 55). Postgenal ridge nearly vertical from hindmost bulge of eye to sclerotized lower marginal portion of gena; upper portion of gena bare, pruinose, wider in all species but one than the setose sclerotized lower genal margin (Fig. 16). Crossvein dm-cu usually not retracted toward crossvein r-m. ..... ***Olcella*** Enderlein

9 spp.; widespread in North America; Sabrosky 1936

Scutum evenly punctate, without dense median acrostichal and dorsocentral lines of punctures with divergent hairs. Postgenal ridge extending forward diagonally from posteroventral curve of eye to vibrissal angle; lower marginal portion of gena setose, shining, and wide, exposing a narrow to sublinear bare upper portion of gena (Fig. 19). Crossvein dm-cu often retracted about its own length from crossvein r-m; crossvein r-m well beyond midpoint of cell bm + dm ..... ***Dasyopa*** Malloch

2 spp.; southern half of U.S.A.

45. Hind femur enlarged, with ventral groove or channel flanked by rows of short peg-like denticles; hind tibia curved, with two rows of short appressed bristles, and fitting against enlarged femur between rows of denticles (Fig. 62) 46

Hind femur and tibia without ventral armature, and slender and straight, though hind femur usually slightly thickened compared with other femora 47

46. First flagellomere short, suborbicular, at most less than 1.4 times as long as broad; arista slender, brown to blackish, with basal segments yellow to brown and only slightly enlarged .... ***Meromyza*** Meigen

23 spp.; widespread in North America; Fedoseeva 1971, 1978

First flagellomere elongate, 1.8–5.0 times as long as broad (as in Fig. 27); arista white, densely pubescent, appearing thickened, with basal segments yellow, long, and thick .... ***Neodiplotoxa*** Malloch

2 spp.; Manitoba to Arizona and Mexico; Becker 1912 (in *Diplotoxa*)

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[3] An undescribed species of *Biorbitella*, atypical in having a thinly pruinose ocellar triangle, also keys to *Incertella*, but can be distinguished by the two pairs of fronto-orbital bristles (see couplet 26).

47. Ocellar triangle with two to several regular or irregular rows of piliferous punctures on each side (Fig. 8), but if these apparently reduced to one row on each side, then row well removed from margin of triangle. Hind tibia slender, without tibial organ 48

Ocellar triangle typically bare of hairs, at most with one row on extreme sides of triangle, but if with two rows (as in some *Thaumatomyia* and *Cetema*), then hind tibia with large oval tibial organ 49

48. First flagellomere or pedicel, or both, more or less elongate (Figs. 8, 28); arista white, densely pubescent, and appearing thickened, with its base yellow, long, and thick. Frons in most species projecting well in front of eye as seen in profile (Fig. 8) ....***Ectecephala*** Macquart

5 spp.; widespread in U.S.A.; Sabrosky 1941*a*

First flagellomere small, broader than long or suborbicular (Fig. 30); pedicel not elongate; arista slender, micropubescent, blackish. Frons only slightly projecting ....***Homaluroides*** Sabrosky

9 spp.; widespread in U.S.A.; Sabrosky 1980*b*

49. Crossvein dm-cu absent (Fig. 41) ....***Elliponeura*** Loew

2 spp.; Quebec and U.S.A.; Sabrosky 1935

Crossvein dm-cu present 50

50. Crossveins r-m and dm-cu approximated, separated by less than length of crossvein dm-cu; cell bm + dm abbreviated (Fig. 42) 51

Crossveins r-m and dm-cu separated by more than length of crossvein dm-cu; cell bm + dm not abbreviated (as in Fig. 40) 52

51. Fronto-orbital setae short, weak, numerous (six to nine in each row). Eye large; greatest length barely greater than width; long axis only slightly diagonal ....***Diplotoxa*** Loew

7 spp.; widespread in North America; Becker 1912

Fronto-orbital setae strongly developed, two or three pairs present. Eye appearing narrowed and elongate, 1.4 times as long as wide; long axis strongly diagonal, situated above axis of vertical to vibrissal angles ....***Pseudopachychaeta*** Strobl

1 sp., *approximatonervis* (Zetterstedt); Holarctic, widespread in North America

52. Head and thorax entirely black. Hind tibia with tibial organ. Small species, 1.75–2.0 mm long ....***Trigonomma*** Enderlein

1 sp., *fossulatum* (Loew); southern Texas, Neotropical

Head partly yellow; ground color of thorax yellow to red with black or reddish stripes and spots, in a few species with scutum black and unstriped. Hind tibia with or without tibial organ. Mostly larger species 53

53. Scutellum flat dorsally, sharply margined (atypical in *parviceps* (Malloch) and *pulla* (Adams)), with bases of apical scutellar bristles approximated (Fig. 51). Hind tibia posterodorsally with a large, conspicuous, elongate, oval tibial organ (Fig. 60) ......***Thaumatomyia*** Zenker

13 spp.; widespread in North America; Sabrosky 1943

Scutellum not flattened and sharply margined; in doubtful cases apical scutellar bristles not approximated or tibial organ absent. Hind tibia with or without tibial organ, but if present this organ linear or at least narrow (Fig. 61) 54

54. Scutum rugose, black, unstriped, with hairs arising from wart-like tubercles that are often star-shaped 55

Scutum appearing smooth, with black or reddish stripes, but in a few species unstriped, with fine inconspicuous piliferous punctures 56

55. Mid tibia with strong preapical ventral spur (Fig. 63); hind tibia with an elongate narrow tibial organ (Fig. 61). Thorax in Nearctic species slender, narrower than head ....***Cetema*** Hendel

2 spp.; widespread in southern Canada and U.S.A.

Mid tibia with a short, weak, apical to preapical ventral bristle (Fig. 64); hind tibia cylindrical, without tibial organ. Thorax not slender ....***Epichlorops*** Becker

3 spp.; widespread in Canada and northern U.S.A.

56. Three pairs of long erect fronto-orbital bristles present; ocellar and postocellar bristles strong; postocellar bristles cruciate. Ocellar triangle typically long and narrow, widely separated from eyes at base (Fig. 11) .... ***Lasiosina*** Becker

3 spp.; widespread in Canada and northern U.S.A.

Numerous weak, hair-like fronto-orbital setae present; ocellar and postocellar bristles weak, hair-like, short, inconspicuous; postocellar bristles parallel to convergent. Ocellar triangle typically broad at base and more narrowly separated from eyes 57

57. First flagellomere typically 1.4–2.0 times longer than broad (Fig. 29); pedicel also elongated, especially dorsally; arista white, densely pubescent and thus appearing thickened, with its base yellow and thickened .... ***Parectecephala*** Becker

6 spp.; chiefly eastern, 1 sp. southwestern; Becker 1912 (part in *Anthracophaga*)

First flagellomere orbicular or suborbicular (Fig. 30), occasionally subquadrate, at most barely longer than broad; pedicel short and rounded; arista of most species blackish with black base, whitish in a few species but rarely with yellow base, and base not thickened. Rarely head and antenna elongated (*Chlorops stigmaticalis* Becker, with deeply grooved ocellar triangle) 58

58. Ocellar triangle dull, heavily pruinose .... ***Anthracophaga*** Loew

1 sp., *declinata* Becker; Colorado to New York, south to Texas and North Carolina

Ocellar triangle shining, without pruinescence except at most on ocellar tubercle .... ***Chlorops*** Meigen

35 spp.; widespread in North America; Becker 1912

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CRYPTOCHETIDAE

100

J. F. McALPINE

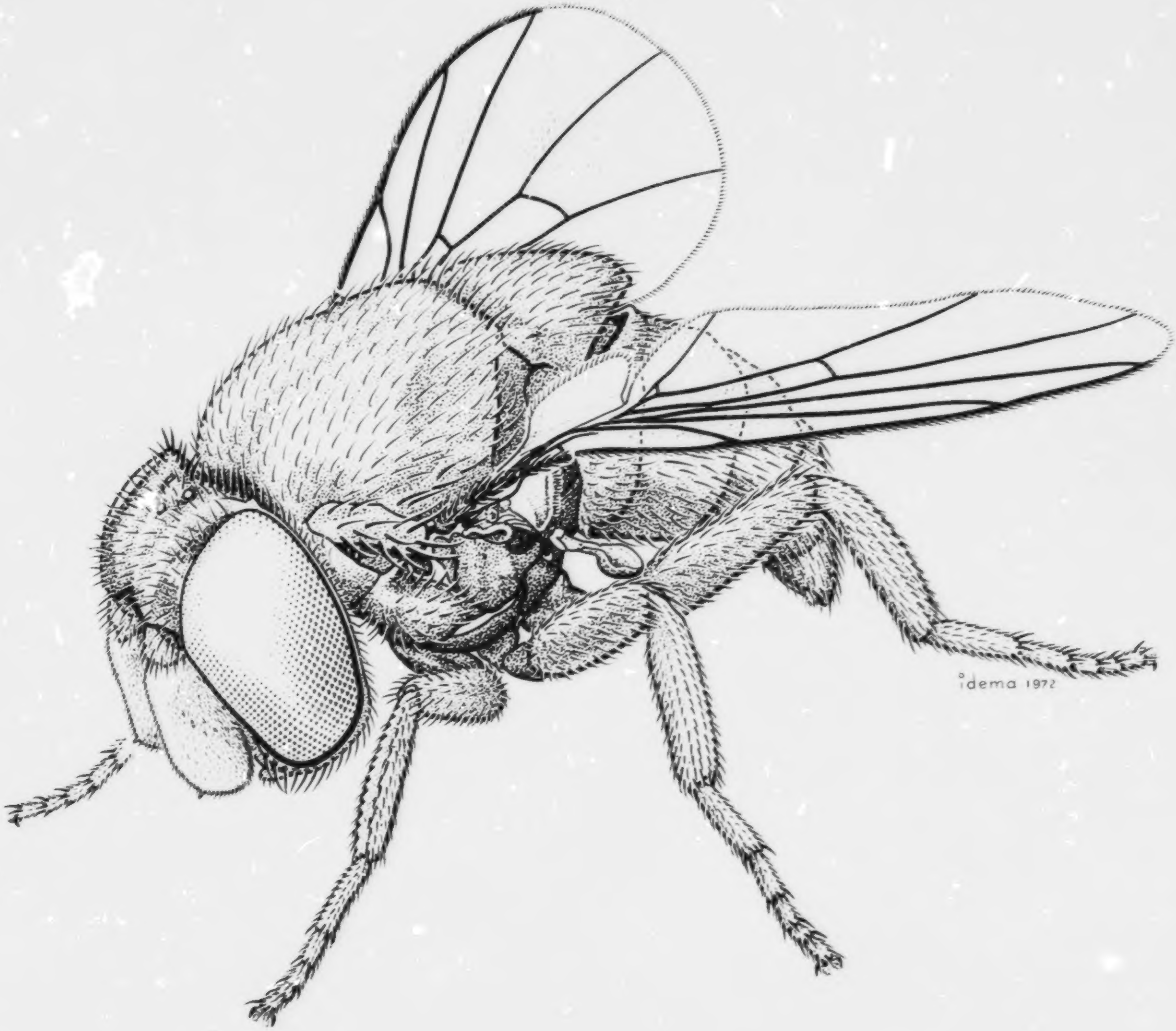

Fig. 100.1. Adult female of *Cryptochetum iceryae* (Williston).

Small stout-bodied flies (Fig. 1), 2–4 mm long, metallic blue black in color, with a broad high head and clear wide wings; first flagellomere very elongate and without an arista. Only one species known in North America, *Cryptochetum iceryae* (Williston), introduced in California from Australia on which the following description is based.

Adult. Head: at least as broad as thorax and twice as high as wide (Fig. 1). Frons nearly square in both sexes, coarsely and densely setulose throughout, with principal bristles scarcely distinguishable; ocellar triangle very large, occupying most of frons, extending to lunule; lunule concealed. Gena very narrow compared with height of eye, with numerous short setulae, without an outstanding oral vibrissa. Face gently convex, uniformly sclerotized, without median carina or membranous sulcus. Clypeus small. Mouthparts and palpus rather small in relation to size of head. Compound eye very large, high oval, occupying most of side of head, distinctly but shortly pubescent. Antenna large; scape and pedicel short; pedicel without a distinct notch or seam on inner dorsal surface, without usual outwardly directed dorsal bristle; first flagellomere greatly enlarged, reaching to lower level of face, almost as broad as face, unusually pubescent throughout; no elongate arista present, but apicodorsal angle with a small peg-like sensory spine that may be a vestige of a true arista (D. K. McAlpine 1976).

Thorax: scutum densely setulose throughout, with principal bristles scarcely distinguishable and the setulae not or indistinctly serially arranged; scutellum unusually large and convex with sharp margins at sides and apex, uniformly setulose above with apical setulae somewhat outstanding, bare below; subscutellum very strongly developed; prescutellum absent. Postpronotum small, crowded anteriorly and flattened in transverse plane; propleuron with a low ridge (propleural carina) in center continuing dorsally from point where prosternum fuses with it, as in Chloropidae. Notopleuron mainly occupied by lateral extension of prescutum. Anepisternum setulose; remaining pleural sclerites including katepisternum bare. Prosternum bare, large, and transverse, extending laterally in front of coxae and fused with propleuron, i.e. precoxal bridge present. Metasternal area linear, bare. Anterior spiracle rather small and round as in Chloropidae.

Wing short and wide (Fig. 1), about twice as long as broad, with strong anal angle. C setulose but not spinose, usually ending at insertion of R_{4+5} but sometimes extending to M_{1+2} (not in Nearctic species), usually with costagial break (proximal to humeral crossvein), humeral break, and subcostal break; Sc with apical half reduced to a fold in membrane; cells bm and dm confluent, i.e. crossvein bm-cu absent; crossvein dm-cu far removed from posterior margin of wing, and seldom more than one-third as long as last section of CuA_1; cell cu*p* imperfectly formed; A_1 reduced to a fold in membrane; A_2 unusually strongly developed, lying close to anal margin of wing, and traceable to wing margin. Halter short, with whitish stem and black knob.

Legs stocky (Fig. 1), setulose but lacking outstanding bristles. Ventral apex of mid tibia, especially, with corona of short bristles; hind tibia with velvety sensory area on posterodorsal surface, as in Chloropidae.

Abdomen: short and broad (Figs. 1, 2, 5). Six well-developed tergites in both sexes; last tergite considerably longer than preceding ones, especially in male where it is possibly a composite of segments 6–8. Sternites 1–5 much reduced (Fig. 2); basal three or four sternites more or less atrophied; apparent sternite 6 of male well-developed, similar to apparent sternites 4 and 5 in female. Both male and female with a single functional spiracle, the sixth, located in the membrane at posterolateral margin of tergite 6.

Male with a single symmetric dorsal sclerite between tergite 5 and epandrium. Epandrium (Fig. 3) reduced to a very thin band dorsally, with sides broadest in middle, with few or no setulae. Surstylus fused to ventral extremities of epandrium, lobate to very reduced, usually setulose at apex (Figs. 2, 3). Cerci rather large, decumbent (Fig. 3). Hypandrium U-shaped, open posteriorly (Figs. 2, 5); gonopods lobe-like, setulose or bare, asymmetric in *C. iceryae*; parameres large, setulose, partially enveloping aedeagus; aedeagus slender, rigid, more or less C-shaped; aedeagal apodeme, at juncture with aedeagus, with two arms projecting around phallobase (Figs. 4, 5); ejaculatory apodeme fairly reduced.

Female (Figs. 5, 6) with tergite and sternite of segment 7 fairly unmodified, free at sides. Sternite and tergite of segment 8 highly modified; posterior margins of sternite 8 produced to form a curved, spine-like, piercing ovipositor. Cerci reduced, fused medially, to form an anus-bearing lobe that projects dorsally at base of spine-like ovipositor. One spermatheca present, relatively weakly sclerotized.

Egg. About 0.2 mm long and less than 0.1 mm wide, kidney-shaped.

Larva. Mature form 1.8–3.17 mm long, ovoid, yellowish white, tapered to anterior end, with 10 clearly marked segments behind head (Fig. 7); each segment bearing a belt of minute spines; terminal segment with a pair of tails 6–9 mm long believed to be gills for absorbing oxygen from blood of host (Thorpe 1931, 1934, 1941*b*). Cephalopharyngeal sclerites with well-developed mandibles and U-shaped dental sclerite; hypopharyngeal sclerite very small; hypostomal sclerite absent; tentoropharyngeal sclerite well-developed. Anterior spiracle retractile into cavity in body wall, with 5–12 elongate digits; digits more or less fused into dart-like structure in Nearctic species. Posterior spiracles forming a pair of posteroventrally curved hooks situated on heavily pigmented plates on dorsoposterior surface of segment 10. The developmental cycles and structures of the larvae differ significantly in their details in different species (for summary see Nartshuk 1981).

Puparium. Brownish black, with 10 clearly visible segments. Operculum formed from first three segments; line of dehiscence extending dorsally only, and not ventrally, on segment 3. Anterior spiracular processes attached to operculum; posterior spiracular processes projecting from adjoining surfaces. Terminal tails shrunken and brittle, easily broken off.

Figs. 100.2–10. *Cryptochetum iceryae* (Williston) and *C. yokohama* Kuwana: (2) ventral and (3) left lateral views of male terminalia; (4) left lateral and (5) ventral views of male terminalia, showing details of aedeagus and associated parts; (6) entire abdomen of male, left lateral view; (7) entire abdomen of female, ventral view; (8) withdrawn and (9) exposed positions of ovipositor, left lateral view; (10) mature larva of *C. yokohama* (not Nearctic).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; aed gd, aedeagal guide; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; prct, proctiger; st, sternite; sur, surstylus; syntg, syntergite; tg, tergite.

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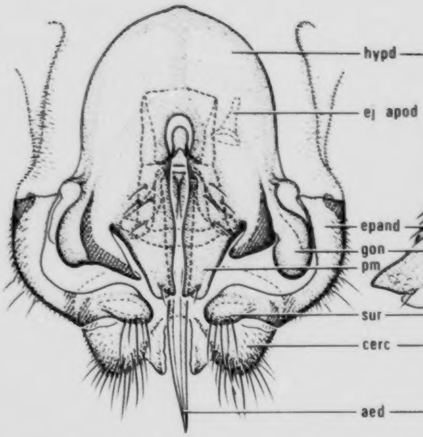
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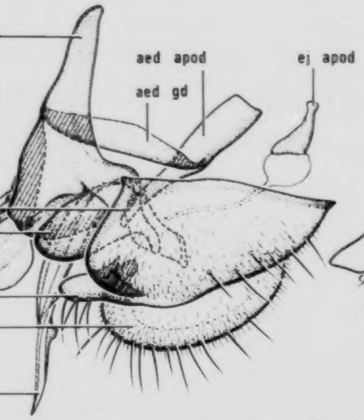
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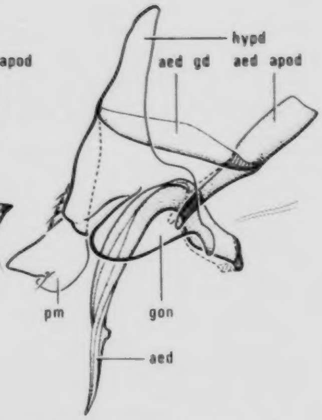
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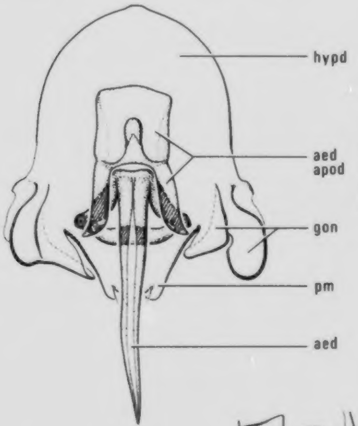
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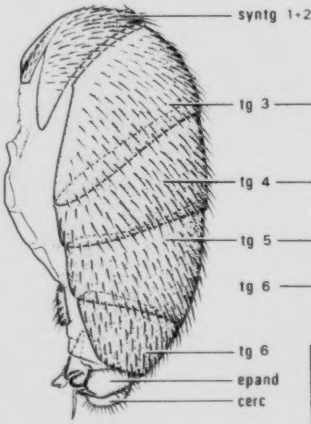
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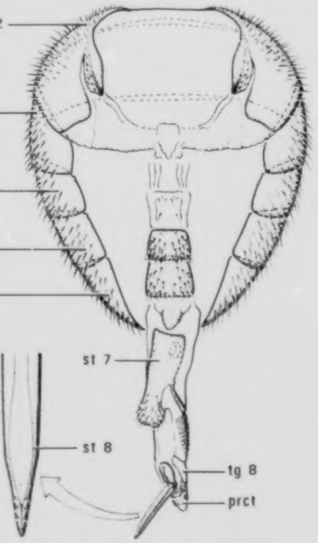
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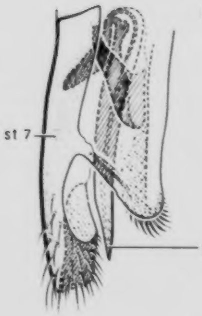

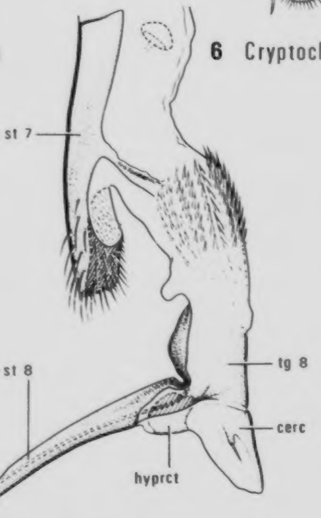
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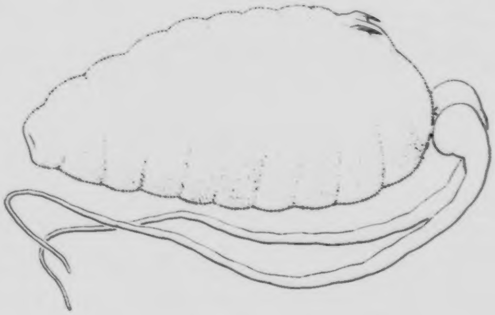
8 ♂ Cryptochetum iceryae **9** ♂



10 Cryptochetum yokohama

Biology and behavior. The immature stages are adapted for endoparasitism in bodies of scale insects (monophlebine scales). They are described in detail by Thorpe (1931, 1934, 1941*a*). The family is not endemic in the New World. However, the remarkable efficacy of the introduced Australian species, *Cryptochetum iceryae*, in controlling the cottonycushion scale, *Icerya purchasi* Maskell, in California makes this case one of the most successful examples of biological control on record.

Classification and distribution. The family consists of *Cryptochetum* Rondani, with four poorly differentiated subgenera (Van Bruggen 1960), and possibly *Phanerochaetum* Hennig from Baltic amber (Hennig 1965), and the peculiar Australian genus *Librella* D.K. McAlpine (D. K. McAlpine 1976). The first genus has been referred to many families, including the Agromyzidae, Carnidae, Chamaemyiidae, Drosophilidae, Milichiidae, and Oscinidae (Chloropidae), by various authors. It resembles the Chloropidae in many apomorphic characters such as enlarged ocellar plate, enlarged prothoracic sternum with precoxal bridge, propleural carina, densely setulose body, peculiarly bristled notopleuron, small round prothoracic spiracle, enlarged convex sharply margined and setulose scutellum, velvety sensory area on hind tibia, strongly reduced abdominal sternites, reduced nonsclerotized spermatheca, chloropid-type male terminalia, peculiar "eye-gnat" habits of adults, and association of larvae with Homoptera. On the other hand, it also resembles certain Milichiidae in some of these, and in additional features. For example, the enlarged ocellar triangle, the enlarged prosternum with precoxal bridge, the propleural carina, the velvety sensory area on the hind tibia, and the reduced weakly sclerotized spermatheca are characters shared with both Milichiidae and Chloropidae. In addition, the wing is very similar to that of Milichiidae and unlike that of Chloropidae in the following respects: C has a humeral break as well as a subcostal break, Sc is greatly weakened on the apical half, but continues as a fold in the membrane, cell cu*p* is present (although imperfectly formed), A_1 ends at the end of cell cu*p*, and A_2 is long and clearly visible. Also, the pleural region below the wing base is strikingly similar to that of the milichiid genus *Eusiphona* Coquillett in a number of ways. For example, the posterodorsal corner of the anepisternum is sharply inflexed and its external surface lies at right angles to that of the anepisternum; there is an unusually deep, sharply defined indentation at the posteroventral angle of the anepimeron; and there are two ear-like lobes at the upper margin of the anepimeron, a larger anterior one in the position of the greater ampulla, and a smaller posterior one behind and below this position. The conclusion is reached that Cryptochetidae is best recognized as a separate family related to both Milichiidae and Chloropidae. Its peculiar combination of characters indicate that it originated more recently than the Milichiidae and earlier than any Chloropidae.

About 25 species are known, mainly from the Ethiopian and Australasian regions; a few occur in the Palaearctic region (Nartshuk 1981); none is endemic in the New World. One fossil species, *Phanerochaetum tuxeni* Hennig from Baltic amber, was assigned to the family (Hennig 1965, 1969). It agrees with *Librella demetrius* D.K. McAlpine (McAlpine 1976) from Australia and differs from other recent cryptochetids in possessing a short arista. Probably, both of these latter species are more closely related to Drosophilidae than to Cryptochetidae (see discussion by J. F. McAlpine, Ch. 116).

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TETHINIDAE

101

J. R. Vockeroth

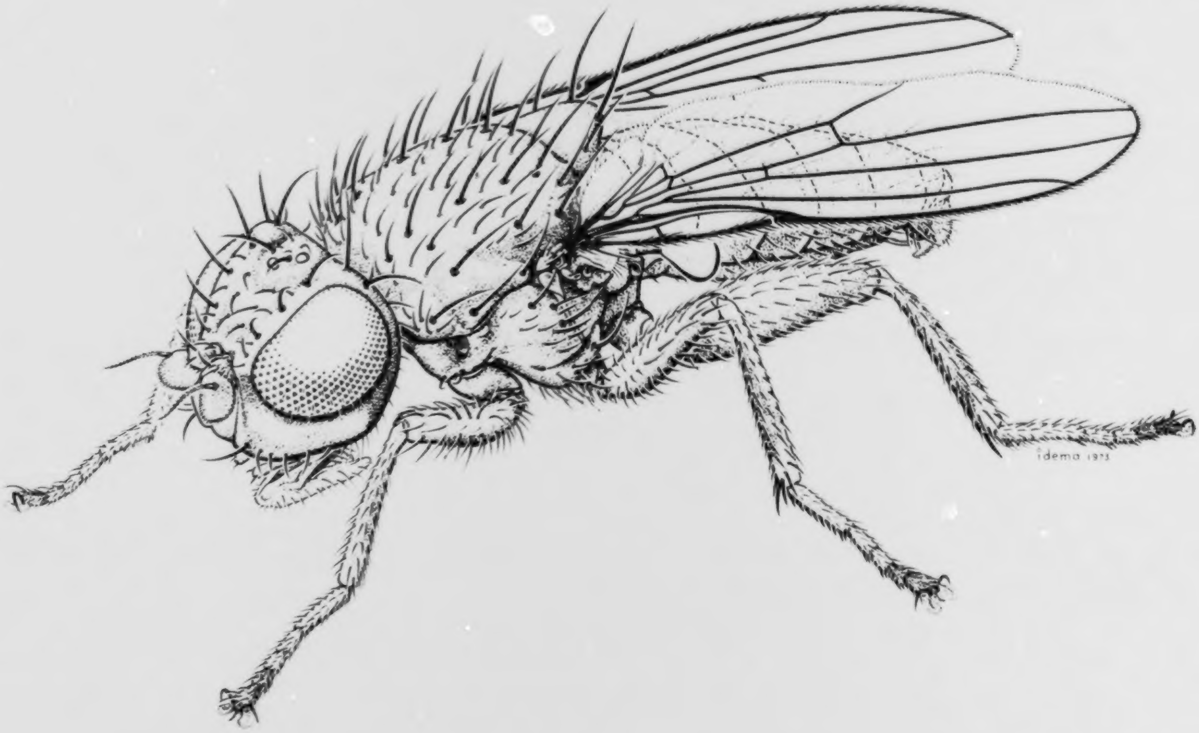


Fig. 101.1. Male of *Tethina parvula* Loew.

Small robust flies, 1.6–3.0 mm long, yellow, gray, or blackish, usually densely pruinose, with wing usually unmarked but rarely having slightly clouded crossveins.

Adult. Head: usually slightly higher than long and subquadrate (Figs. 2, 3, 5, 7), sometimes produced forward below and subtriangular in profile (Fig. 4). Frons about as long as its maximum width, slightly to strongly narrowed anteriorly, of same width in both sexes; intrafrontal area usually bare or with a few minute hairs, in *Tethina* Haliday with two to six pairs of strong and usually cruciate frontal hairs; orbital plates extending to anterior end of frons. Chaetotaxy: one to three reclinate orbital bristles usually present on upper two-thirds or less of orbital plate, often accompanied by a few additional short hairs, but in *Tethina* a series of four or five lateroclinate orbital bristles present decreasing in length anteriorly and extending almost to antenna with an irregular number of shorter medioclinate bristles below and medial to these; ocellar and inner and outer vertical bristles strong; postocellar bristles absent; inner occipital bristles moderately strong to minute, slightly to strongly convergent. Face slightly to strongly narrowed, with a weak depression below each antenna, and with a slightly protruding median ridge; parafacial narrow, bare. Gena from about one-eighth to seven-tenths height of eye; lower margin of gena with a row of weak to strong hairs usually becoming stronger anteriorly, with anteriormost hairs strong and vibrissa-like; area above this ventral row of hairs either bare or with scattered fine hairs; a small shining or subshining callus sometimes present anteriorly just above vibrissa-like bristle; a narrow shining ridge curving upward anteriorly and extending dorsally to middle of length of face sometimes evident along entire lower margin of gena. Eye round to obliquely oval, bare or with minute scattered hairs. Antenna short, usually slightly drooping; first flagellomere subcircular; arista with extremely short hairs. Proboscis short to moderately long depending on length of lower margin of head; labella fleshy or variously slender and elongate; palpus of moderate length, slightly enlarged toward apex.

Thorax: normal in form; prosternum bare, triangular, strongly broadened anteriorly, joined to propleuron by a narrow precoxal bridge; scutellum almost twice as broad as long, rounded apically; metasternal area bare, short, transverse. Chaetotaxy: one postpronotal bristle, one presutural intra-alar bristle, two notopleural bristles, one presutural and three postsutural dorsocentral bristles, one supra-alar bristle, and two postalar bristles present; acrostichal bristles multiseriate or biseriate, bristle-like or hair-like, or absent; scutum, apart from strong bristles, nearly bare or (especially in *Tethina*) with few to many weak to strong hairs; scutellum without hairs, but with two pairs of marginal bristles, although basal pair sometimes weak; proepisternum, and usually proepimeron, each with one moderate to very weak bristle; anepisternum with one or more bristles posteriorly and with setulae or hairs at least near posterior margin; katepisternum with one strong posterodorsal bristle and with setulae or hairs varying in number and distribution; pleura otherwise bare.

Wing clear, whitish or slightly brownish, rarely with faint crossvein clouds. Anal angle and alula well-developed. C unspined, broken only near apex of Sc; other veins without setulae; Sc either complete but very close to R_1 apically or in contact with or fused with extreme apex of R_1; cell bm and cell dm fused or separated; position of crossvein r-m variable; cell cu*p* present but small; A_1 variable, either virtually absent, moderately distinct but short, or extending as a weak fold about two-thirds distance to wing margin; A_2 long, clearly visible but little sclerotized.

Legs slender, with only femora sometimes slightly swollen. Fore coxa either about one-half as long as fore femur and not extending posteroventrally to mid coxa, or about three-quarters as long as fore femur and extending to or almost to mid coxa. Coxae and femora with a few weak bristles; tibiae without distinct bristles except usually for an apical ventral bristle on mid tibia and sometimes an apical anteroventral bristle on hind tibia.

Abdomen: subcylindrical, slightly tapering. Tergite 1 slightly shorter than tergite 2; sternite 1 very small, bare. Tergites and sternites 2–5 unmodified, weakly bristled; spiracles 1–5 each situated in membrane below its respective tergite.

Male terminalia (Figs. 13, 14) symmetric. Tergite 6 and sternite 8 fused into a single dorsal sclerite behind tergite 5, with line of fusion very faint; synsclerite either longer or shorter than tergite 5; relative lengths of these two components variable, both haired or bare. Sternites 6 and 7 and tergites 7 and 8 indistinguishable; spiracle 6 below lower margin of tergite 6; spiracle 7 inside anteroventral angle of sternite 8. Epandrium usually with a long broad ventrolateral process resembling a surstylus fused with tergite; this process sometimes deeply divided or with a slender inner lobe; surstylus subcylindrical, slender, projecting posteroventrally behind ventral process of epandrium; in *Tethina* only ventrolateral lobe of epandrium absent and surstylus broad, resembling lobe of other genera, and partially fused with epandrium. Hypandrium very short, anteriorly with a pair of short dorsomedial processes firmly fused with very long slender aedeagal apodeme near posterior end of apodeme; posterodorsal arms of hypandrium articulated with inner arms of surstylus but widely separated from one another; gonopods fused more or less solidly with hypandrium, represented by one or two clusters of setae, and sometimes with a free lobe projecting posteroventrally beside base of aedeagus; parameres lying between lateral arms of hypandrium and base of aedeagus, extending caudally beside base of aedeagus, usually very slender, and apparently at least partly fused with posterior bases of gonopods, but in *Pelomyia* Williston very complex and with several lobes or processes at posterior end; aedeagus with a flattened semicircular base fused to posterior end of aedeagal apodeme, and with a rather elongate slender, slightly twisted, short-haired, tapering distal portion; ejaculatory apodeme large.

Female terminalia (Fig. 8) cylindrical or nearly so. Segment 6 shorter than 5, with spiracle situated in membrane below tergite. Segment 7 variable in length; tergite 7 or sternite 7 sometimes with a strongly sclerotized anterior marginal or submarginal band or with a posterior emargination; tergite 7 sometimes with an anteromedial process; both sclerites sometimes partly or entirely fused anterolaterally; spiracle 7 situated in or just below margin of tergite 7; membrane between segments 7 and 8 longer than segment 7. Segment 8 variable in length; tergite 8 usually subquadrate and emarginate anteriorly, in *Pelomyiella* Hendel and *Neopelomyia* Hendel long and slender and slightly broadened posteriorly; sternite 8 usually divided medially with sclerotized portions slender or broad, in *Pelomyiella* and *Neopelomyia* undivided and shaped like a long slender inverted Y. Epiproct and hypoproct distinct. Cercus subcylindrical or compressed, from two to six times as long as broad, in at least one species of *Tethina* with short strong setulae. Two spermathecae present, subspherical.

Larva. Unknown for Nearctic genera, described for two species of the subantarctic genus *Apetaenus* Eaton; best descriptions given by Séguy (1940) and Hardy (1962). Cuticle strongly spiculate. A transverse row of four to eight dorsal tubercles present on each segment from mesothorax to penultimate abdominal segment. A many-branched tree-like anterior spiracle present; each posterior spiracle borne on a long tapering process with a strong tubercle below this process.

Biology and behavior. Little is known of the biology, although most species occur on marine shores or in saline areas. Melander (1952) gives notes on the adult habitats of many Nearctic species. At least one Nearctic species of *Tethina* visits flowers. Larval habitats are not definitely known. *Horaismoptera hennigi* Sabrosky was abundant on seaweed in Sri Lanka; the larvae may live there (Sabrosky 1978). Harrison (1959) surmises that the larvae of *Macrocanace littorea* (Hutton) live in penguin dung because the adults are associated with colonies of penguins and other birds. Hardy (1962) reports adults and larvae of *Apetaenus watsoni* Hardy found under rookery stones, so this species too may be associated with birds. The Nearctic genera, however, certainly have no association with birds; adult habitats suggest that larvae live in soil or possibly in algal masses.

Classification and distribution. The family is world wide in distribution, occurring on the major continents and on many oceanic islands. Fewer than 100 species have been described, mostly from the Holarctic region, but many more probably exist. *Tethina* (including *Phycomyza* Melander) occurs in all major faunal regions, *Pelomyia* is Holarctic and

Neotropical, and *Pelomyiella* is Holarctic. Two genera, *Neopelomyia* and *Masoniella* Vockeroth, are known only from the Nearctic region.

The description of adults given above is based on the Nearctic species. The six exotic genera show some marked differences; many of these are discussed by Sabrosky (1978). *Dasyrhicnoessa* Hendel, widespread in the Pacific area, resembles *Tethina* but has the eye with short dense hairs. *Pseudorhicnoessa* Malloch, from Taiwan, has C ending at R_{4+5}. *Horaismoptera* Hendel, from the Indian Ocean and southern Africa, and *Tethinosoma* Malloch, from New Zealand, have strong irregular costal spines; these two genera had previously been referred to a total of six different families (Sabrosky 1978). Three nominal genera occurring on subantarctic islands (*Apetaenus*, *Listriomastax* Enderlein, and *Macrocanace* Tonnoir & Malloch), previously placed in the Coelopidae or Canacidae, were referred to the Tethinidae by Griffiths (1972). The first two were synonymized by Hennig (1971); I think *Macrocanace* could reasonably be considered another synonym. Two species of *Apetaenus* have the wings greatly reduced; the third, *A. litoreus* (Enderlein), has macropterous and brachypterous individuals. *A. litoreus* and *Macrocanace australis* (Hutton) have the abdomen of the female (but not of the male) greatly modified; *A. litoreus* has tergite 1 enormously enlarged and swollen, and *M. australis* has segments 1 and 2 very elongate. The two genera can be distinguished from other Tethinidae by the enlarged and protruding clypeus; as in *Horaismoptera*, but not in other Tethinidae, A_1 extends to the wing margin.

Melander (1952) revised the Nearctic species; this work is not cited in the key here under each genus. Foster (1976) discussed the relationship of the Nearctic genera and described several new species; his work, plus my own observations, indicates that a study of male terminalia will disclose additional unrecognized species, especially in *Pelomyia*.

The relationship of the family to others is still unclear. Griffiths (1972) implied a relationship with Chloropidae and Milichiidae; Hennig (1971) accepted this possibility, but thought the family was closer to the Anthomyzoidea; later, Hennig (1973) listed the Tethinidae as a family of uncertain relationships. No fossils are known.

Key to genera

1. Gena bare except for a ventral row of hairs or weak bristles (Figs. 2, 3). Acrostichal hairs in two or more complete or nearly complete rows 2

Gena with few to many scattered hairs between eye and ventral row of hairs or bristles (Figs. 4, 5, 7). Acrostichal hairs sparse or absent 3

2. Gena about one-eighth height of eye (Fig. 2); two strong orbital bristles present; orbital plate and frons otherwise with only a few very short hairs. Cells bm and dm confluent (Fig. 9). Fore coxa about three-quarters as long as fore femur; hind tibia without apicoventral bristle . . . . **Masoniella** Vockeroth

1 sp., *richardsi* Vockeroth; southern California, inland

Gena at least one-third height of eye (Fig. 3); three to five orbital bristles present; orbital plate with strong setulae among bristles; frons with two rows of strong interfrontal setulae. Cells bm and dm separate (Fig. 10). Fore coxa not more than one-half as long as fore femur; hind tibia with strong apicoventral bristle (Fig. 6) . . . . **Tethina** Haliday

15 spp.; widespread, coastal; Foster 1976 (partial key)

3. Vibrissal angle not projecting; lower margin of head short and convex; eye rounded; one or two orbital bristles present (Figs. 5, 7) 4

Vibrissal angle strongly projecting; lower margin of head long and nearly straight; eye oblique; three orbital bristles present (Fig. 4) . . . . **Neopelomyia** Hendel

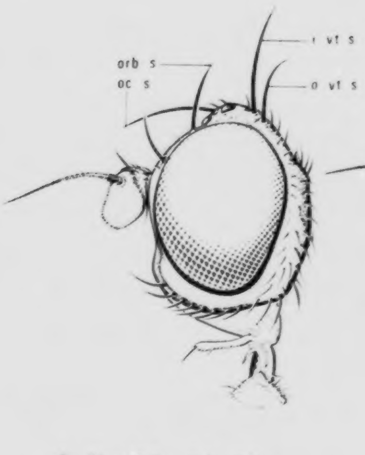
2 spp.; Pacific coast; Foster 1976

4. Lower margin of gena and facial ridges with a narrow strongly sclerotized shining strip; one large fronto-orbital bristle present near midlength of frons (Fig. 5). Crossvein r-m near middle of cell dm; last section of CuA_1 not longer than crossvein dm-cu (Fig. 11) . . . . **Pelomyia** Williston

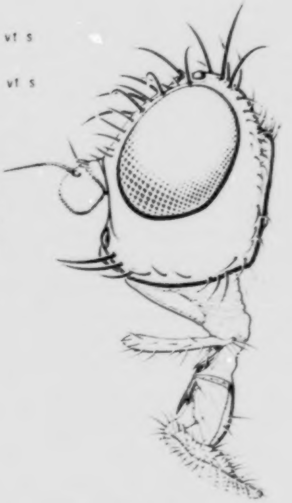
3 spp.; widespread, coastal and inland

Lower margin of gena and facial ridges without shining stripe; two orbital bristles present on upper half of frons, the anterior one sometimes short (Fig. 7). Crossvein r-m well beyond middle of cell dm; last section of CuA_1 two or three times as long as crossvein dm-cu (Fig. 12) . . . . **Pelomyiella** Hendel

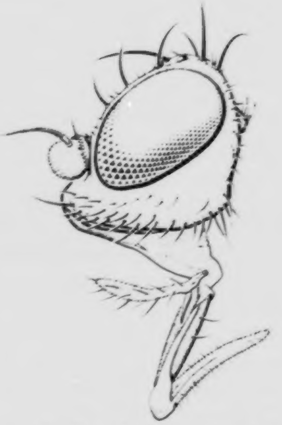
3 spp.; coastal and inland in west, coastal only in east



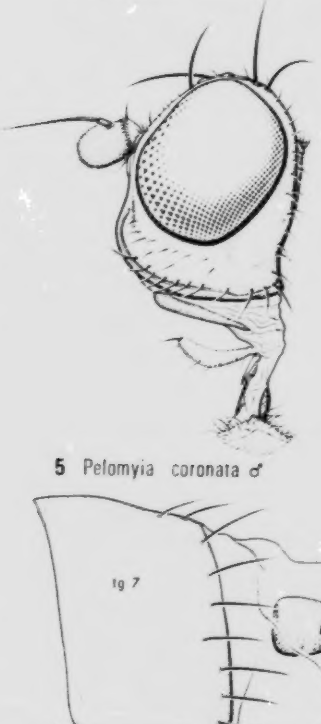
2 Masoniella richardsi ♂



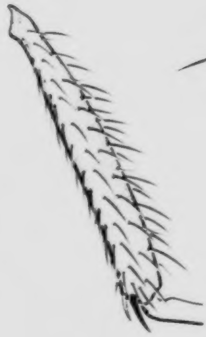
3 Tethina horripilans ♂



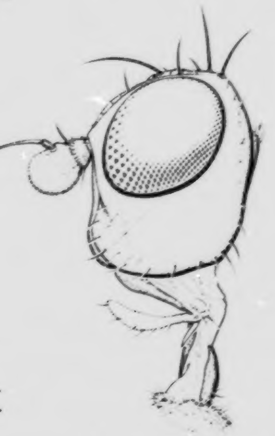
4 Neopelomyia rostrata ♂



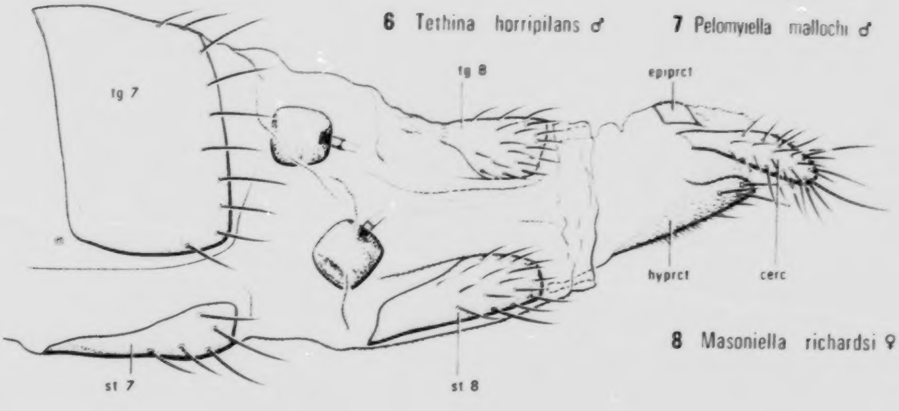
5 Pelomyia coronata ♂



6 Tethina horripilans ♂



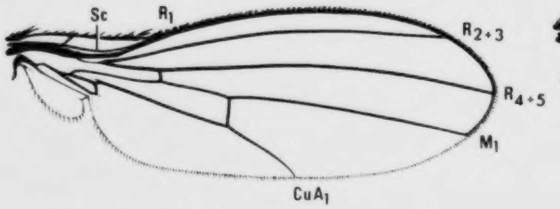
7 Pelomyiella mallochi ♂



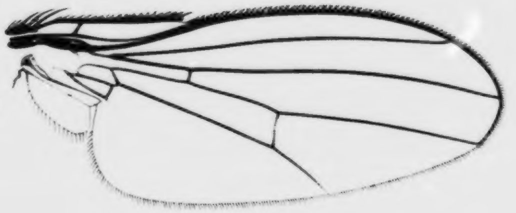
8 Masoniella richardsi ♀

Figs. 101.2–8. Heads, tibia, and terminalia: heads of (2) *Masoniella richardsi* Vockeroth, (3) *Tethina horripilans* (Melander), (4) *Neopelomyia rostrata* (Hendel), and (5) *Pelomyia coronata* (Loew); (6) hind tibia in anterior view of *Tethina horripilans*; (7) head of *Pelomyiella mallochi* (Sturtevant); (8) terminalia of *Masoniella richardsi*.

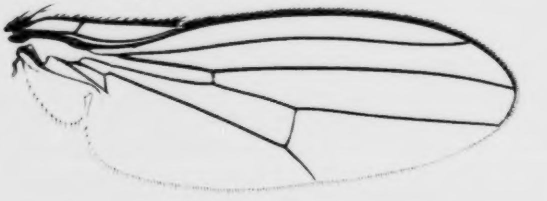
Abbreviations: cerc, cercus; epiprct, epiproct; hyprct, hypoproct; i vt s, inner vertical seta; oc s, ocellar seta; orb s, orbital seta; o vt s, outer vertical seta; st, sternite; tg, tergite.


Sc
R1
R2+3
R4+5
M1
CuA1

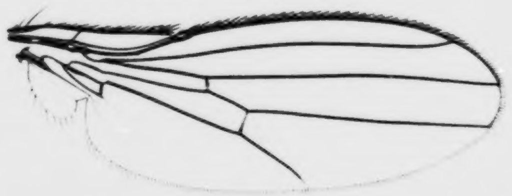
9 Masoniella richardsi ♂



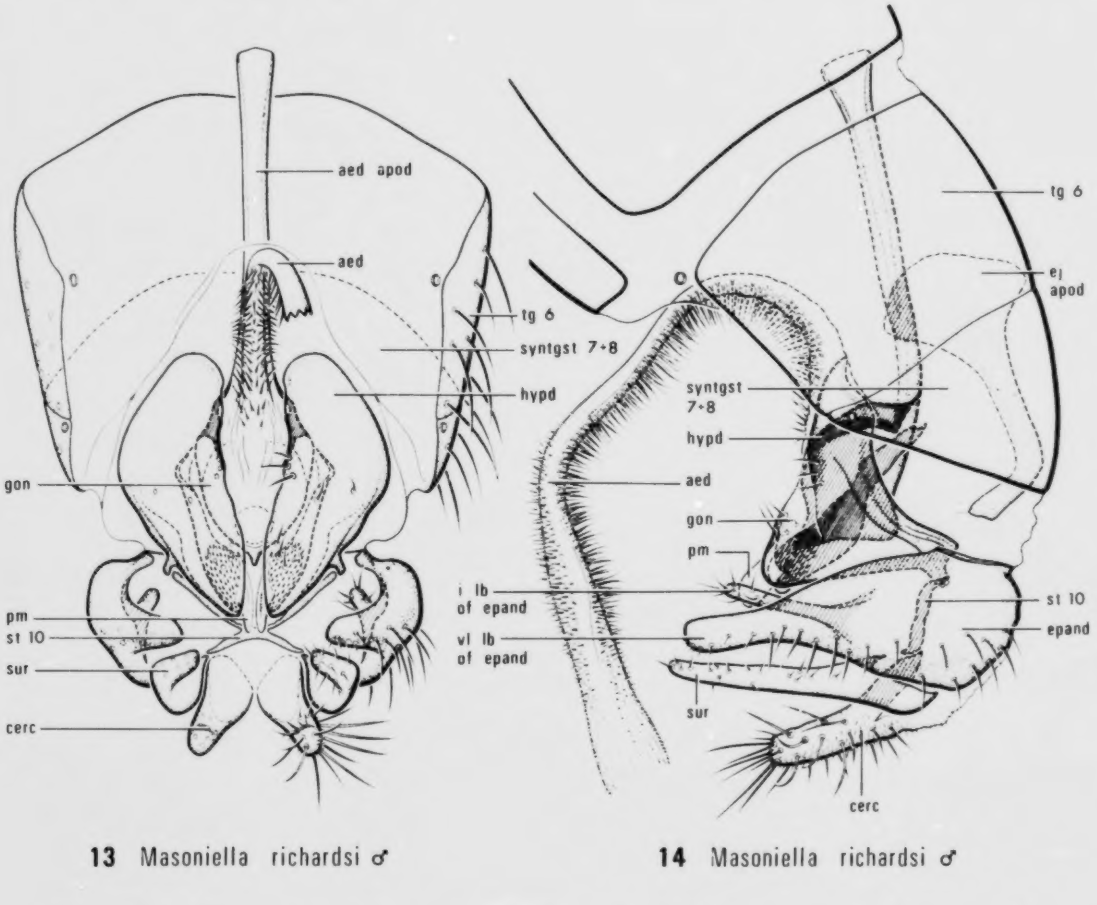
10 Tethina horripilans ♂



11 Pelomyia coronata ♂



12 Pelomyiella mallochi ♂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13 Masoniella richardsi ♂

14 Masoniella richardsi ♂

Figs. 101.9–14. Wings and terminalia: wings of (9) *Masoniella richardsi* Vockeroth, (10) *Tethina horripilans* (Melander), (11) *Pelomyia coronata* (Loew), and (12) *Pelomyiella mallochi* (Sturtevant); (13) ventral aspect and (14) lateral aspect of terminalia of male of *Masoniella richardsi*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; i lb of epand, inner lobe of epandrium; pm, paramere; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; vl lb of epand, ventrolateral lobe of epandrium.

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CANACIDAE

102

WILLIS W. WIRTH

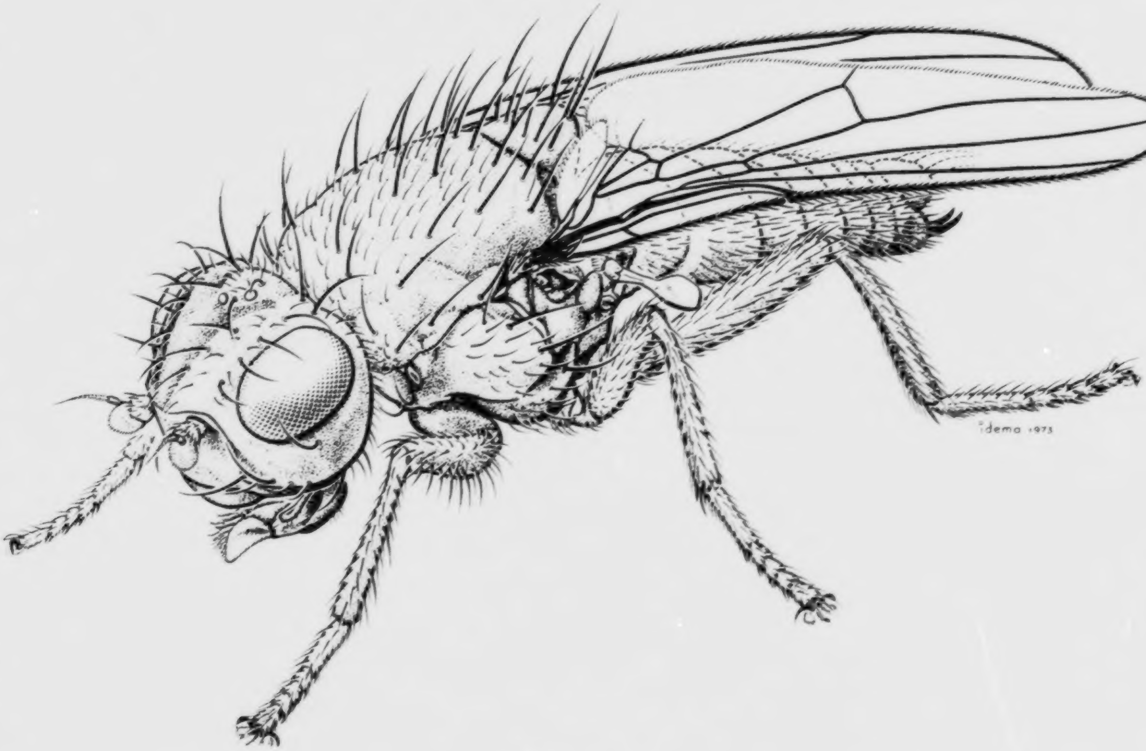


Fig. 102.1. Female of *Canacea macateei* (Malloch).

Small pruinose flies (Fig. 1), 3-5 mm long; blackish, brownish, yellowish, or gray in color, often with striking whitish to grayish pruinescence ventrally; wing usually without color pattern.

Adult. Head: large, with large subcranial cavity (Figs. 2, 4). Clypeus prominent, usually fitting into emargination on lower margin of face. Proboscis large, with fleshy labella; palpus well-developed. First flagellomere rounded; arista dorsal, short pubescent to bare. Frons wide in both sexes; three to five pairs of divergent fronto-orbital bristles present; frontal vitta often differentiated, with or without one or more pairs of interfrontal bristles. Ocellar triangle large; ocellar bristles present and strong; postocellar bristles absent, but often replaced by pseudopostocellar bristles, i.e. specialized ocellar setulae; inner and outer vertical bristles strong. Face slightly convex to concave; upper portion swollen, separating antennae; bristles usually lacking except for an incurved vibrissa. Gena broad; one or more upcurved genal bristles present, usually in an oblique series; subvibrissal setulae present or absent.

Thorax: four or more pairs of dorsocentral bristles present (Fig. 1); prescutellar acrostichal bristles present or absent; one pair of postpronotal bristles, one or two pairs of notopleural bristles, and one pair of presutural and usually two pairs of postsutural supra-alar bristles present; sometimes one pair of presutural intra-alar bristles present; anepisternal and katepisternal bristles present or absent; one or two pairs of scutellar bristles present. Legs rather short, without strong bristles; femora sometimes with ventral armature of short stout spines. Wing (Fig. 6) with C extending to M; Sc complete and separate from R_1 almost to its tip; C with only subcostal break; cells br, bm, dm, and cu*p* complete; A_1 short.

Abdomen: Male (Fig. 3) with terminalia symmetric. One pregenital segment present, formed mostly by tergite 6 but with its posterior portion possibly consisting of remnants of segments 7 and 8; sternite 6 absent; spiracles 1-6 situated just below margins of respective tergites; spiracle 7 situated in posterior part of tergite 6. Epandrium short or nearly divided medially. Surstylus fused with epandrium, in repose directed anteroventrally below abdomen, with its apex simple, hooked, or bilobate. Hypandrium broadly open or nearly closed anteriorly, posteriorly usually with a pair of lateral arms extending above aedeagus and fusing to form a backwardly directed long and acute or short and blunt spine-like process; gonopod large, weakly sclerotized, with dense fine setae; paramere rather slender, with a few preapical setae; aedeagus short, with complex sclerotization; aedeagal apodeme slender and very long. Cercus distinct but weak.

Female (Fig. 5) either with tergite 7 fused with sternite 7 and with sternite 7 divided medially and spiracle 7 enclosed in the synsclerite (*Canacea* Cresson), or with tergite and sternite 7 separate, and with sternite 7 large and entire and spiracle 7 situated below the margin of the tergite (*Canaceoides* Cresson, *Nocticanace* Malloch). Tergite 8 large; sternite 8 divided medially or nearly so, each half weak except posteriorly where it bears several strong straight or curved setae. Epiproct and cerci completely fused; cerci apparently represented by a pair of long, backwardly directed, closely appressed, tapering, sometimes strongly sclerotized lobes (genital lamellae of authors); each lobe ending in a very strong seta that may be acute or blunt and flattened and may be preceded by one or more similar but smaller setae. Hypoproct small, with or without distinct hairs. Ventral wall of genital chamber with V-shaped or ring-shaped sclerite. Two spermathecae present, variable in shape.

Egg. Simple and ovoid; white with fine microscopic reticulations on chorion.

Larva. Larvae of six species are known: three of *Procanace* Hendel and two of *Canaceoides*, all from Hawaii (Hardy and Delfinado 1980), and *Canacea macateei* (Malloch) from Massachusetts (Teskey and Valiela 1977). The following account is based mainly on a description by Teskey and Valiela (1977) of *C. macateei*.

Larva (Fig. 7) 5–6 mm long, creamy white to yellowish, resembling those of most acalyptrate Diptera, but body tapering both anteriorly and posteriorly from about fourth abdominal segment and terminating in a slender retractable respiratory tube about 1 mm long when extended. Abdominal segments 2–7 each with a slightly raised transverse ventral creeping welt. Prothoracic spiracle in form of a slender retractable filament about 1 mm long when fully extended; several pairs of nearly sessile spiracular openings present, more or less alternating on opposite sides of apical half of filament. Posterior spiracles (Fig. 9) situated at the apex of a respiratory tube, separated by a narrow furrow; each with three oval spiracular openings arranged with longitudinal axis of each opening at slightly less than right angles to adjacent opening; each spiracular plate with four tufts of short interspiracular setae. Cephalopharyngeal skeleton (Fig. 8) with ventral cornu truncated and appearing broken at apical margin; a complex series of six pairs of small sclerites, including the dental and labial sclerites, present below the hypopharyngeal sclerite; mandibles close together anteriorly, separated posteriorly by a small V-shaped accessory oral sclerite; anterior ventrolateral extensions of tentoropharyngeal sclerite narrowly fused with ventral bridge of hypopharynx; parastomal bars prominent, united to each other by a thin fenestrated epipharyngeal sclerite.

The larva of *Canaceoides angulatus* Wirth, illustrated by Williams (1938) as *Canace nudata* Cresson, differs from that of *C. macateei* in having a well-developed perianal pad bearing numerous strong claw-like hooks, in having about 10 spiracular openings mounted on christmastree-like stalks on each anterior spiracle, and in lacking ventral creeping welts.

Puparium. Brown, very similar in size and form (Fig. 10) to mature larva, rather spindle-shaped, curved at each end; integumental spinules more prominent than on the larva and anterior respiratory processes fully extended.

Biology and behavior. Canacids are almost exclusively intertidal in habit. Only eight fresh-water species are known, the larvae of which live in torrential mountain streams of Hawaii and the Orient, and probably New Guinea. The feeding habits of adults and larvae are poorly known, but Williams (1938) stated that the larva of *Canaceoides angulatus* is saprophytic or perhaps a feeder on living algae.

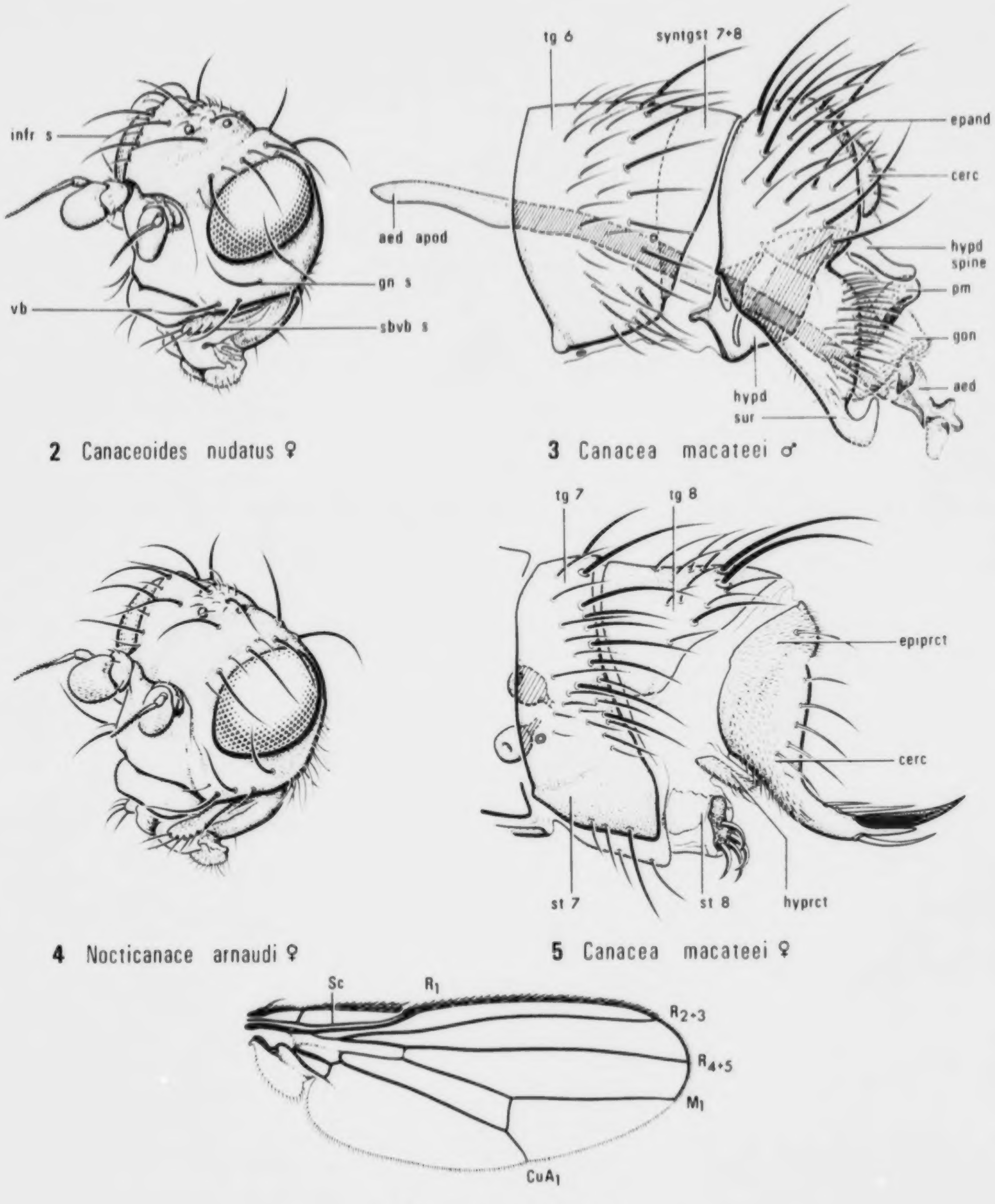
Classification and distribution. The Canacidae were previously included in the Ephydridae or considered to be closely related to them, even after Sturtevant (1926) showed that the two groups had very dissimilar female reproductive systems. Hennig (1958) considered the family to be closely related to the Milichiidae and Tethinidae. Griffiths (1972) and Hennig (1973) were doubtful about a close relationship with the former family and left the Canacidae as an unplaced family.

The Canacidae comprise about 101 species in 11 genera. They occur on warm temperate or tropical coasts and are particularly abundant in the Pacific, with no fewer than 12 species in the Galapagos Islands. The genus *Macrocanace* Tonnoir & Malloch, from islands south of New Zealand, was correctly referred to the Tethinidae by Griffiths (1972). The only wordwide revision (Wirth 1951) treated only 32 species and is quite out-of-date. Wheeler (1952) reviewed the Nearctic species. No fossil Canacidae are known.

Keys to genera

Adult

1. Four lateroclinate fronto-orbital bristles present; frontal vitta with at least two pairs of long interfrontal bristles; pseudopostocellar bristles strong. Prescutellar acrostichal bristles present; acrostichal hairs numerous, in four irregular rows (Fig. 1). Female cercus with one large apical seta which is usually acutely pointed (Fig. 5) .... ***Canacea*** Cresson
2 spp.; Atlantic coast, California; Mathis 1982, Wirth 1970


infr s
vb
gn s
sbvb s
aed apod
tg 6
syntgst 7+8
epand
cerc
hypd spine
pm
gon
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sur
tg 7
tg 8
epiprct
cerc
st 7
st 8
hyprct
Sc
R_1
R_{2+3}
R_{4+5}
M_1
CuA_1

2 Canaceoides nudatus ♀

3 Canacea macateei ♂

4 Nocticanace arnaudi ♀

5 Canacea macateei ♀

6 Canacea macateei ♀

Figs. 102.2–6. Heads, terminalia, and wing: Heads of (2) *Canaceoides nudatus* (Cresson) and (4) *Nocticanace arnaudi* Wirth; (3) male terminalia, lateral view, of *Canacea macateei* (Malloch); (5) female terminalia, lateral view, of *Canacea macateei*; (6) wing of *Canacea macateei*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; epiprct, epiproct; gon, gonopod; gn s, genal bristle; hypd, hypandrium; hypd spine, hypandrial spine; hyprct, hypoproct; infr s, interfrontal bristle; pm, paramere; sbvb s, subvibrissal bristle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite; vb, vibrissa.

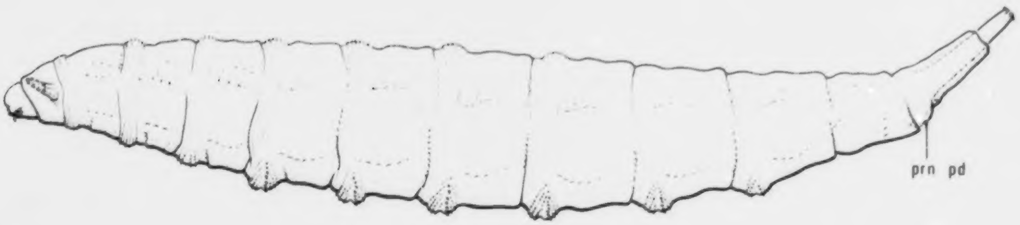
Three lateroclinate fronto-orbital bristles present; frontal vitta with one pair of interfrontal bristles just in front of level of anterior ocellus; pseudopostocellar bristles weak or absent (Figs. 2, 4). Prescutellar acrostichal bristles absent; acrostichal hairs few, at most two weak pairs present near scutellum. Female cercus with two large setae, one apical and one subapical, each rather bluntly rounded 2

2. Gena with three strong equally developed bristles in an oblique line posterior to vibrissa (Fig. 2) .... ***Canaceoides*** Cresson

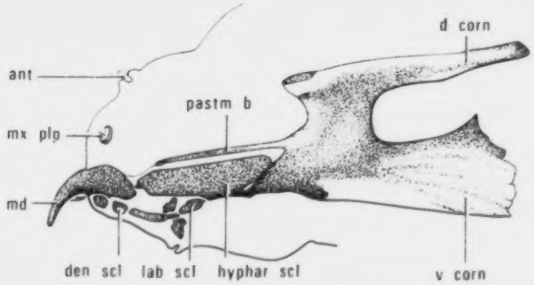
1 sp., *nudatus* (Cresson); California; Wirth 1969

Gena with two strong upcurved bristles posterior to vibrissa and with one or more fine subvibrissal setulae below and between these (Fig. 4) .... ***Nocticanace*** Malloch

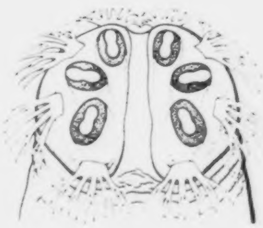
2 spp.; southern Atlantic coast, California; Wirth 1954



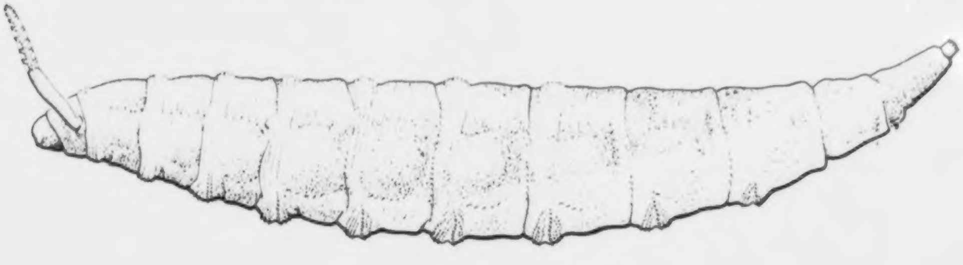
7 Canacea macateei



8 Canacea macateei



9 Canacea macateei



10 Canacea macateei

Figs. 102.7–10. Immature stages of *Canacea macateei* (Malloch): (7) larva; (8) cephalopharyngeal skeleton; (9) posterior spiracles of larva; (10) puparium.

Abbreviations: ant, antenna; d corn, dorsal cornu; den scl, dental sclerite; hyphar scl, hypopharyngeal sclerite; lab scl, labial sclerite; md, mandible; mx plp, maxillary palpus; pastm b, parastomal bar; prn pd, perianal pad; v corn, ventral cornu.

Larva

1. Anterior spiracle with sessile openings (Fig. 7). Body cuticle smooth, with minute spinules restricted to narrow segmental bands and distinct ventral creeping welts (Fig. 7). Perianal pad greatly reduced, with a single spine .... ***Canacea***

Anterior spiracle with openings on long papillae. Body cuticle more uniformly covered with dense coarse spicules and granulations; ventral creeping welts absent. Perianal pad with numerous claw-like hooks .... ***Canaceoides***

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SCATHOPHAGIDAE

103

J. R. VOCKEROTH

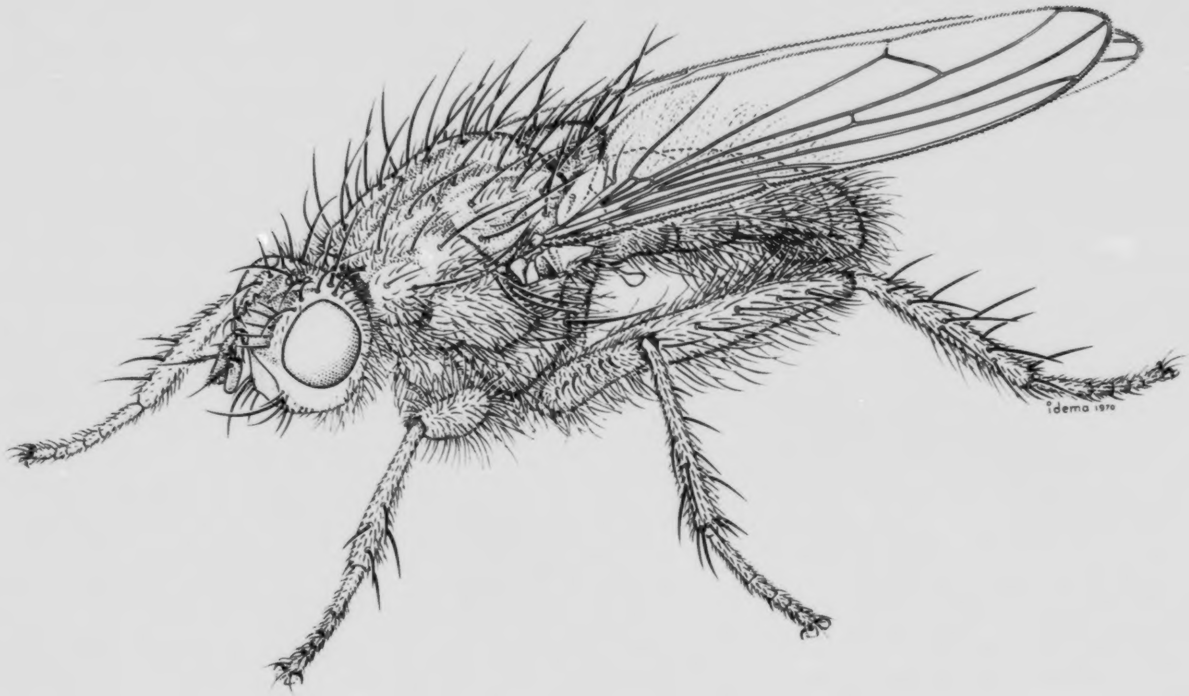


Fig. 103.1. Male of *Scathophaga stercoraria* (Linnaeus).

Slender, strongly to weakly bristled and sometimes densely hairy flies (Fig. 1), usually black, gray, brown, or yellow, sometimes strikingly bicolored, usually subshining but sometimes densely gray to yellow pruinose. Wings usually clear, but sometimes with clouded crossveins, spots, or transverse bands. Male abdomen often enlarged apically. Length 3–11 mm.

Adult. Head: usually higher than long (Figs. 2–13), subpentagonal with well-developed postcranium and with face sometimes strongly receding below. Frons usually of equal width in both sexes, about one-third as wide as head, very rarely slightly narrower in male than in female; fronto-orbital plate much narrower than frontal vitta. Bristles of frons the same in both sexes; one to six medioclinate frontal bristles and one proclinate to lateroclinate and one or two proclinate, reclinate, or lateroclinate orbital bristles present; few to many hairs or weak bristles often interspersed among strong bristles; interfrontal bristles absent but frontal vitta sometimes with minute hairs; ocellar, postocellar, and inner and outer vertical bristles present; bristles of head extremely short only in *Hydromyza* Fallén (Fig. 11). Parafacial bare; vibrissal angle with strong to weak vibrissa and few to many weaker bristles and hairs; facial ridge bare; gena narrow to very broad, its lower margin with a row of weak to strong subvibrissal bristles. Postcranium with many fine hairs on lower half; these hairs usually pale but sometimes partly or entirely dark. Eye bare. Antenna (Figs. 14–19) with first flagellomere two to five times as long as wide, usually rounded apically but sometimes with anterodorsal angle subacute (Fig. 19), sometimes with a long slender bristle near base of arista (Fig. 16); arista straight or rarely elbowed, bare to plumose, usually longer than first flagellomere, three-segmented; first aristomere short; second aristomere up to five times as long as wide; third aristomere long and tapering; scape and pedicel short; pedicel with a distinct dorsal seam. Palpus well-developed, often with a long apical seta (Figs. 6, 7), sometimes (especially in male) broadened toward apex (Fig. 8), spoon-shaped, strap-like, or with strong lateral setae; labella rather small, with strong prestomal teeth.

Thorax: bristles usually distinct and moderately strong, but discal bristles sometimes very short or weak and scarcely distinguishable from abundant scutal hairs. Postpronotum usually with one or two bristles, rarely without bristles, sometimes also with short erect black setulae (Fig. 22). Scutum with two to many rows of fine acrostichal hairs, and usually with the following bristles: two presutural and three postsutural dorsocentral bristles, two presutural intra-alar bristles (often called the posthumeral and presutural), and two notopleural, two postsutural intra-alar, two postsutural supra-alar (the anterior one often called the prealar), and two postalar bristles; some of these bristles sometimes very weak or absent; scutellum with one or two, or rarely more, pairs of submarginal bristles, without ventral hairs. Laterotergite usually bare, rarely with fine erect hairs; proepisternum haired or bare on disc, and with one or more hairs and usually also bristles on lower convex part; proepimeron usually with fine hairs, sometimes also with a weak bristle; anepisternum (Figs. 20, 21) with a row of posterior bristles, usually haired on posterodorsal half or less (Fig. 21), but sometimes haired on most of its surface (Fig. 20); katepisternum usually with one posterodorsal bristle, sometimes with two or three variously arranged bristles or without a distinct bristle, sometimes with weak ventral bristles, with variously distributed hairs; anepimeron and katepimeron haired or bare. Postcoxal bridge usually absent (Fig. 24), rarely present (Fig. 23). Prosternum haired or bare; metasternal area bare.

Wing (Figs. 25–29) with venation nearly constant; veins, except C and sometimes upper surface of R_1, without setae; C with costagial, humeral, and subcostal breaks; supernumerary crossveins present between R_{4+5} and M in some males of *Pogonota* Zetterstedt; supernumerary crossveins present in brown spots on membrane in *Ernoneura* Becker; extreme apex of M curved forward in some species of *Pogonota*; crossvein bm-cu absent in the Nearctic species of *Hydromyza*; A_1 usually complete but sometimes ending before wing margin. Lower calypter linear, i.e. with posterior margin straight, not at all convex.

Legs (Figs. 30–35) usually slender, with weak to very strong bristles. Fore femur and tibia sometimes with short strong black setulae below; femora and tibiae of males sometimes highly modified. First tarsomere of hind tarsus sometimes with a distinct subbasal ventral bristle.

Abdomen: slender, sometimes strongly enlarged apically in males (Figs. 38–42). Tergites and sternites 1–5 well-developed; tergites 1 and 2 fused; sternite 1 usually haired.

Male with sternites 3 and 4 sometimes broadened or otherwise modified and with distinctive hairing (Fig. 38). Sternite 5 usually deeply bilobate posteriorly (Fig. 40), the lobes sometimes highly modified or projecting ventrally (Fig. 42), markedly asymmetric in some species of *Allomyella* Malloch, more rarely with posterior margin of sternite nearly straight and with a pair of submedian processes. Segments 6–8 asymmetric; tergite 6 dorsal in position, in the Scathophaginae with bristles and hairs, usually well-developed and free from syntergosternite 7 + 8 (Fig. 41), but rarely fused with it; in the Delininae tergite 6 short, bare, firmly fused with syntergosternite 7 + 8 (Fig. 39); sternite 6 strongly asymmetric, usually fused with sternite 5, but in *Neochirosia* Malloch separated from it by membrane, usually lying mostly or entirely on the left side of the mid line, fused laterally with the reduced sternite 7 and left lateral in position; sternite 7 fused with syntergosternite 7 + 8; syntergosternite 7 + 8 middorsal in position and only slightly asymmetric. Spiracle 1 situated in pleural membrane below tergite 1; spiracles 2–5 usually situated in lateral margins of the corresponding tergites but some or all sometimes in pleural membrane; left spiracle 6 situated in membrane just below left end of tergite 6; left spiracle 7 situated in posterior part of sternite 7; right spiracles 6 and 7 variable in position, in or near lower right margin of tergite 6 and syntergosternite 7 + 8. Epandrium well-developed, sometimes very long, with its posterior surface directed ventrally in repose, sometimes with long hairs or weak bristles. Surstylus well-developed, articulated with epandrium, varied in shape throughout the family, sometimes with long dense setae; the pair of surstyli differing in shape only in *Pleurochaetella* Vockeroth. Hypandrium a rather flat to deep plate forming a complete ring or open posteriorly, articulated laterally to the ventral arm of the epandrium and posterolaterally, either directly or through a bacilliform sclerite, with the inner side of the base of the surstylus; aedeagus well-sclerotized, rather complex, sometimes long and whip-like; basiphallus usually with a distinct epiphallus; aedeagal and ejaculatory apodemes present; gonopod articulated with hypandrium, usually projecting ventrally and with one or more setae, in *Hydromyza* in the form of a bare flat plate; paramere articulated, projecting ventrally, bare or with a few minute setae. Cerci separate or partly or completely fused, varying from simple to subdivided and very complex lobes; in *Pogonota* cerci fused to form a large keeled plate below the epandrium (Fig. 40), cercus sometimes with long dense marginal hairs that may extend above the rest of the abdomen (Fig. 42).

Female with segments 6 and 7 usually mostly exposed (Figs. 36, 37). Ovipositor cylindrical, slightly to strongly compressed especially posteriorly, or rarely depressed. Spiracles 1–5 as in male; spiracles 6 and 7 usually both situated in tergite 6, rarely with one or both in membrane below it or with spiracle 6 in tergite 6 and spiracle 7 in tergite 7. Sclerites of segments 6, 7, and 8 varied in detail; tergites 6, 7, and 8 and sternite 7 entire or medially divided; tergite 7 sometimes entirely membranous; sternite 7, and sometimes sternites 6 and 5, with a slender anterior internal apodeme in *Cordilura* Fallén; sclerites of segment 7 sometimes fused into a ring; sternite 8 almost always medially divided, forming a solid undivided plate only in *Scathophaga mollis* Becker, often heavily sclerotized and acute or toothed apically or with short stout spines, rarely entirely membranous, and with the halves of the sternite sometimes fused with tergite 8; membrane between segments 7 and 8 sometimes enlarged below and with strong scale-like retrorse spines. Proctiger weak, consisting of an entire or divided epiproct, an entire and nearly flat hypoproct, and a pair of weak cerci. Spermathecae usually three in number but two in some Delininae, varying in shape from a sphere to a long nearly straight or coiled tube more than 10 times as long as wide; surface usually ridged, sometimes with very strong constrictions so spermatheca resembles a series of beads of unequal size.

Egg. Elongate oval, pale, usually with a pair of low parallel sublateral flanges ventrally on entire length; in *Scathophaga* Meigen a pair of diverging flanges present on anterior third. Most of egg surface finely reticulate, between flanges more coarsely reticulate.

Larva. Subcylindrical, anteriorly usually tapering but sometimes blunt. Mandibles slender to stout, often toothed below; hypopharyngeal sclerite well-developed; parastomal bars absent; dorsal cornu of tentoropharyngeal sclerite more slender than, and usually longer than, ventral cornu; dorsal cornu with a distinct window posteriorly; ventral cornu with at most an indistinct aperture. Abdominal segments with ventral creeping welts of minute spines; spines sometimes also present dorsally in intersegmental areas, rarely entire cuticle with minute spicules. Terminal segment surrounded by four to eight pairs of tubercles that vary greatly in size and arrangement and offer excellent taxonomic characters. Anterior spiracle (Fig. 43) two-branched, with up to 60 papillae. Posterior spiracle on a short tube, with three straight respiratory slits; in *Cordilura* this tube with one or more slits projecting well beyond margin of spiracular disc; four branched interspiracular hairs present on disc. Neff (1970) gives a key to subfamilies.

Biology and behavior. Known larvae of Delininae are leaf miners in Liliaceae, Orchidaceae, and Commelinaceae. The few known larvae of Scathophaginae have varied habits. Many are phytophagous in a wide variety of plants, especially *Scirpus*, *Juncus*, and *Pedicularis*; several Palaearctic species of *Nanna* Becker are important pests of flower heads of *Phleum* (Borg 1959). Some larvae are predacious, either in plant tissues or in water or wet soil. Larvae of the commonest genus, *Scathophaga*, are coprophagous, feeding in dung of cattle and in rodent burrows and such, or feeding in decaying seaweed, whereby they are restricted to seacoasts. Séguy (1952) summarized known larval habitats; Neff (1968, 1970), Neff and Wallace (1969*a*, 1969*b*), and Wallace and Neff (1971) have published excellent accounts of biology and morphology of immature stages of a number of species.

Eggs of Delininae are attached to the leaf surface; the empty shells remain long after hatching so these species would provide excellent material for population studies. Eggs of Scathophaginae are inserted into plant tissues, dung, or other substrate; the varied ovipositors are apparently highly adapted for this role.

Adults are apparently all predacious on insects or other invertebrates. Mating has been described for *Pogonota* (*Pogonota*) *barbata* (Zetterstedt) (Hackman 1956) and, in great detail, for *Scathophaga stercoraria* (Linnaeus) (Parker 1974 and earlier papers).

Classification and distribution. The Scathophagidae have often been treated as a subfamily of the Muscidae or the Anthomyiidae; family status is reasonable, although the only probable autapomorphic characters of the family so far recognized are the broad frons of the male and the greatly reduced lower calypter (but see McAlpine, Ch. 116). Two subfamilies are recognized. The Delininae, with tergite 6 of the male bare and fused with syntergosternite 7 + 8 and in which the larvae are leaf miners, is probably a monophyletic group. The Scathophaginae, with tergite 6 haired and almost always free from syntergosternite 7 + 8 and with varied larval habits, is possibly paraphyletic.

The family, with about 250 described species, is almost entirely confined to the Holarctic region and is more northern in overall distribution than any other family of Diptera. In the Nearctic region nine genera or subgenera, and about 25 species, are restricted or nearly restricted to arctic tundra. Even more species are primarily subarctic, and the family reaches its greatest diversity at about the latitude of southern Canada. More than 34% of the described Nearctic species are Holarctic in distribution. Only about five species occur south of the equator, in South America and Africa, mostly at high altitudes. In the Oriental region one species occurs in the Malay Peninsula but none are known from Indonesia, New Guinea, or Australia. No species appear to be native to oceanic islands.

Two fossil species of *Cordilura*, *C. vetusta* Heer (Heer 1849) and *C. exhumata* Cockerell (Cockerell 1916), have been described from Tertiary deposits, but their family placement is uncertain.

Key to genera

1. Upper depressed portion of propleuron (disc of proepisternum) with at least a few fine hairs 2

Upper depressed portion of propleuron bare 56

2. Katepisternum with at most one bristle 3

Katepisternum with two or three bristles, the anterior bristle sometimes weak 49

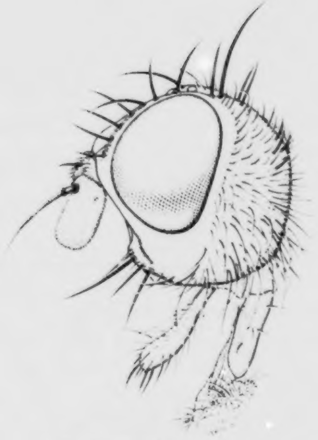
3. Anepisternum uniformly although sometimes sparsely haired over its entire surface, or if with restricted bare areas anteroventrally, at least with hairs of posterior part of sclerite extending broadly to proepimeral area (Fig. 20) 4

Anteroventral third or more of anepisternum bare or with only proepimeral bristle or a few adjacent hairs, or both (Fig. 21) 6

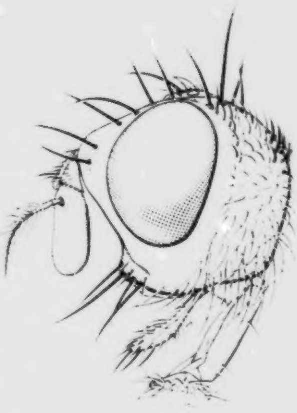
4. Wing with many small round brown spots, some of which enclose supernumerary stump veins (Fig. 25) .... ***Ernoneura*** Becker

1 sp., *argus* (Zetterstedt); Arctic

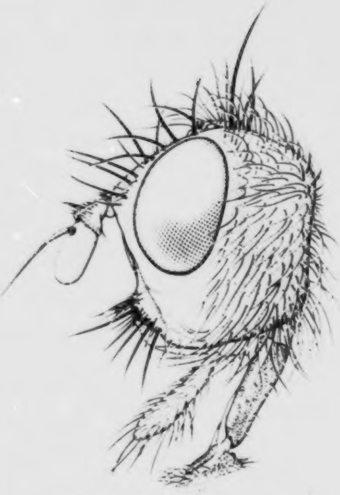
Wing unmarked or with at most crossveins and apices of longitudinal veins darkened 5



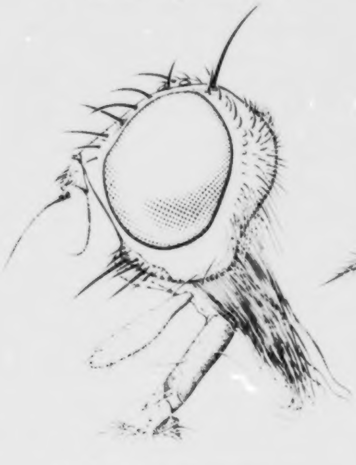
2 Scathophaga furcata ♂



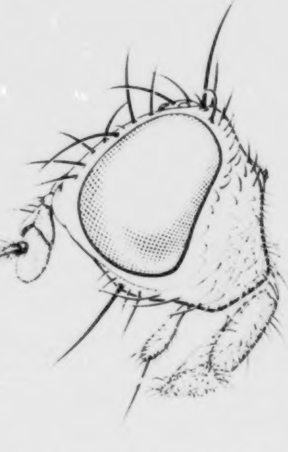
3 Scathophaga reses ♂



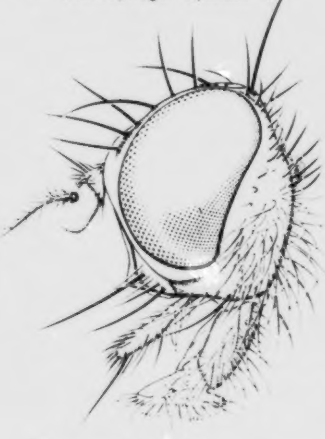
4 Scathophaga apicalis ♂



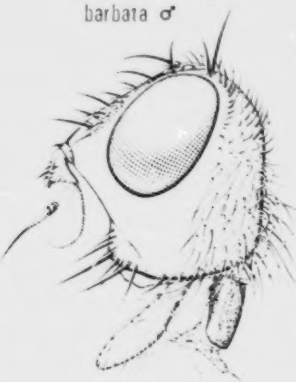
5 Pogonota (Pogonota) barbata ♂



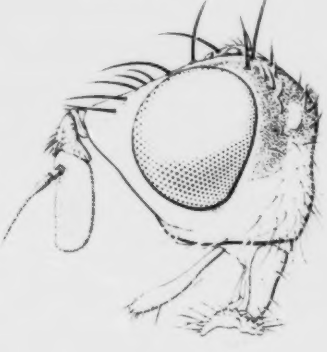
6 Cordilura (Paratidia) criddlei ♂



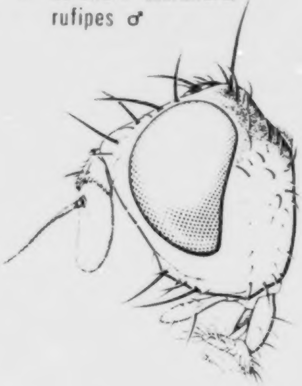
7 Cordilura (Cordilura) rufipes ♂



8 Staegeria sp. ♂

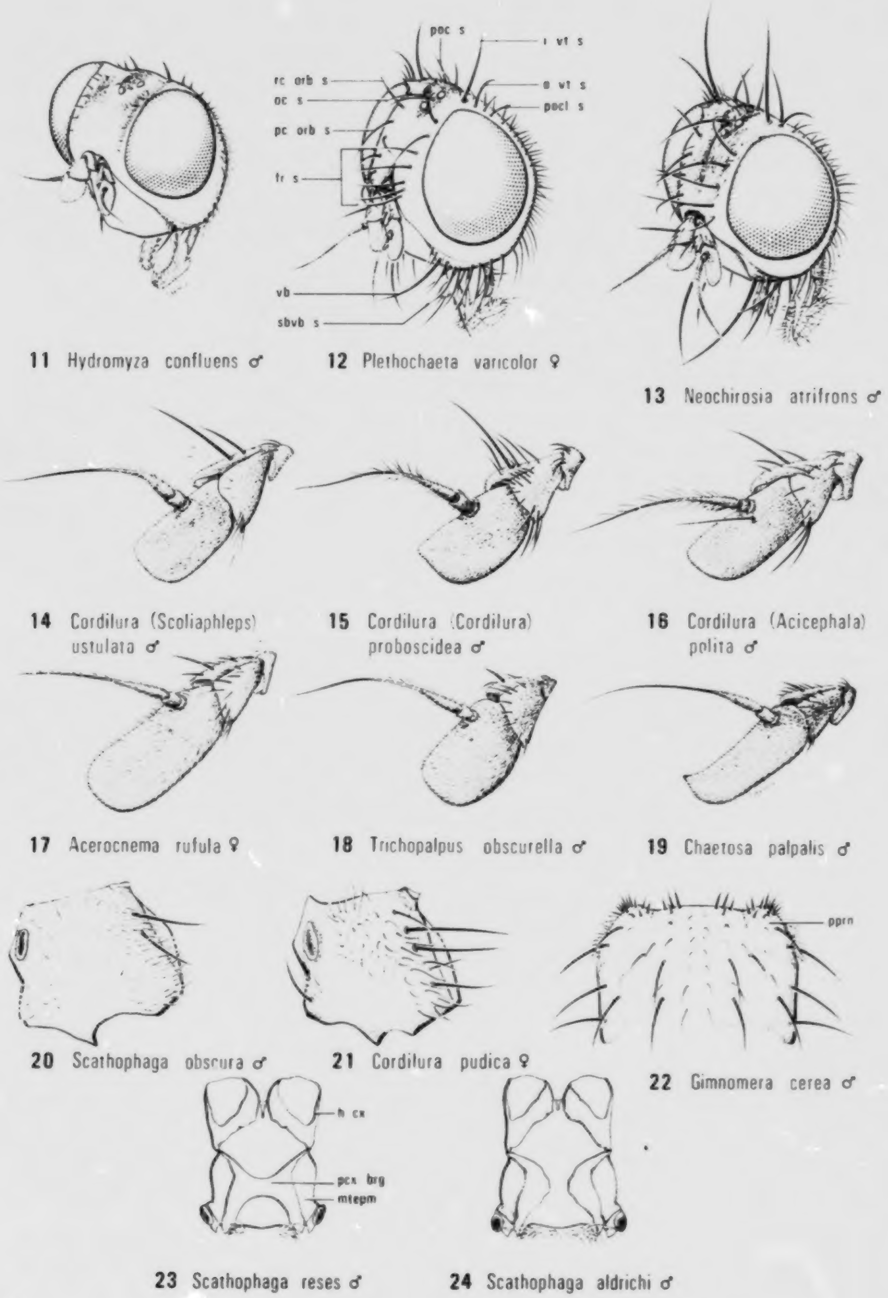


9 Hexamitocera loxocerata ♂



10 Peratomyia vittata ♂

Figs. 103.2–10. Heads: (2) *Scathophaga furcata* (Say); (3) *Scathophaga reses* Giglio-Tos; (4) *Scathophaga apicalis* Curtis; (5) *Pogonota* (*Pogonota*) *barbata* (Zetterstedt); (6) *Cordilura* (*Paratidia*) *criddlei* Curran; (7) *Cordilura* (*Cordilura*) *rufipes* Meigen; (8) *Staegeria* sp.; (9) *Hexamitocera loxocerata* (Fallén); (10) *Peratomyia vittata* (Coquillett).



11 Hydromyza confluens ♂
12 Plethochaeta varicolor ♀
13 Neochirosia atrifrons ♂
14 Cordilura (Scoliaphleps) ustulata ♂
15 Cordilura (Cordilura) proboscidea ♂
16 Cordilura (Acicephala) polita ♂
17 Acerocnema rufula ♀
18 Trichopalpus obscurella ♂
19 Chaetosa palpalis ♂
20 Scathophaga obscura ♂
21 Cordilura pudica ♀
22 Gimnomera cerea ♂
23 Scathophaga reses ♂
24 Scathophaga aldrichi ♂

Figs. 103.11–24. Heads, antennae, and details of thoraces: heads in anterodorsal view of (11) *Hydromyza confluens* Loew, (12) *Plethochaeta varicolor* Coquillett, and (13) *Neochirosia atrifrons* (Coquillett); antennae of (14) *Cordilura (Scoliaphleps) ustulata* Zetterstedt, (15) *Cordilura (Cordilura) proboscidea* Zetterstedt, (16) *Cordilura (Acicephala) polita* (Coquillett), (17) *Acerocnema rufula* (Curran), (18) *Trichopalpus obscurella* (Zetterstedt), and (19) *Chaetosa palpalis* (Coquillett); anepisternum of (20) *Scathophaga obscura* (Fallén) and (21) *Cordilura pudica* Meigen; (22) anterior half of scutum of *Gimnomera cerea* (Coquillett); posteroventral surface of thorax and hind coxae of (23) *Scathophaga reses* Giglio-Tos and (24) *Scathophaga aldrichi* (Malloch).

Abbreviations: fr s, frontal seta; h cx, hind coxa; i vt s, inner vertical seta; mtepm, metepimeron; oc s, ocellar seta; o vt s, outer vertical seta; pc orb s, proclinate orbital seta; pcx brg, postcoxal bridge; poc s, postocellar seta; pocl s, postocular seta; pprn, postpronotum; rc orb s, reclinate orbital seta; sbvb s, subvibrissal seta; vb, vibrissa.

5. Apical half of fore tibia with two strong anteroventral bristles ...... ***Ceratinostoma*** Meade
1 sp., *ostiorum* (Curtis); Atlantic coast, littoral

Fore tibia without anteroventral bristles .... ***Scathophaga*** Meigen, in part
27 spp.; widespread, including Arctic; Malloch 1935, James 1950 (as *Scopeuma* Meigen)

6. Posteroventral apical bristle of hind tibia long and strong, subequal to anteroventral apical bristle. Presutural acrostichal hairs present or absent .... ***Cordilura*** Fallén ... 7

Posteroventral apical bristle of hind tibia short or absent, at most one-fourth as long as anteroventral apical bristle. Presutural acrostichal hairs present 16

7. Arista short pubescent, the longest hairs not longer than greatest diameter of arista and not extending beyond midlength of arista (Fig. 14). Cell r_{2+3} at least slightly broader at level of crossvein r-m than halfway between this point and wing margin (Fig. 26) .... ***Cordilura*** (***Scoliaphleps*** Becker)
1 sp., *ustulata* Zetterstedt; boreal

Arista long pubescent to plumose, the longest hairs longer than greatest diameter of arista and extending to at least three-fifths length of arista (Figs. 15, 16). Cell r_{2+3} not narrowed beyond level of crossvein r-m (Fig. 28) 8

8. A_1 ending abruptly well before wing margin (Fig. 28) .... ***Cordilura*** (***Cordilurina*** James), in part
13 spp.; widespread; Malloch 1923 (as *Parallelomma* Becker), James 1955

A_1 extending at least faintly to wing margin 9

9. First flagellomere with a long fine bristle arising on outer surface below base of arista (Fig. 16). Face strongly receding below (as in Fig. 6) .... ***Cordilura*** (***Acicephala*** Coquillett)
1 sp., *polita* (Coquillett); widespread

First flagellomere without a bristle (Fig. 15). Face vertical (Fig. 7) to strongly receding (Fig. 6) 10

10. Membrane of cells br, bm, and cu*p* partly or completely devoid of microtrichia (Fig. 27) .... ***Cordilura*** (***Achaetella*** Malloch)
2 spp.; widespread

Wing membrane entirely trichose beyond level of crossvein h 11

11. Face slightly to strongly receding below (Fig. 6). Scutellum with one pair of strong bristles, the apical pair short and weak or absent 12

Face vertical or nearly so (Fig. 7) or, if slightly receding, scutellum with two pairs of strong subequal bristles 13

12. Postpronotal bristles absent. Face with shallow shining black antennal grooves .... ***Cordilura*** (***Pseudacicephala*** Malloch)
3 spp.; central and western; Malloch 1931

Postpronotum with at least one distinct bristle. Face without distinct antennal grooves (Fig. 6) .... ***Cordilura*** (***Paratidia*** Malloch)
5 spp.; boreal and western; James 1955

13. Presutural acrostichal hairs absent 14

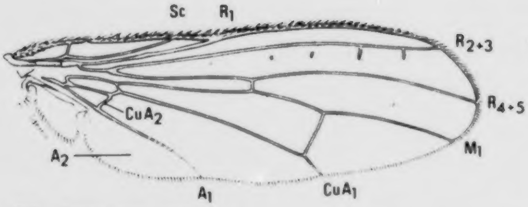
Presutural acrostichal hairs present 15

14. Thorax black, usually densely pruinose .... ***Cordilura*** (***Cordilura*** Fallén), in part
18 spp.; widespread; James 1955

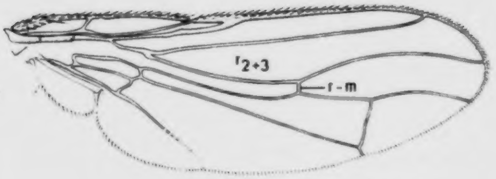
Thorax mostly or entirely shining yellow .... ***Cordilura*** (***Snyderia*** James)
1 sp., *praeusta* Loew; eastern

15. Scutum with two presutural and three postsutural dorsocentral bristles, with the first presutural and first postsutural ones much shorter and weaker than the others; apical scutellar bristles very short, hair-like. Female with each half of sternite 8 with apex slender, acute, and curved slightly upward (Fig. 36) .... ***Cordilura*** (***Cordilurina*** James), in part
see couplet 8

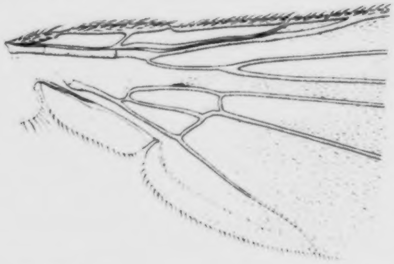
Scutum with two presutural and two or three postsutural dorsocentral bristles, all moderately strong; apical scutellar bristles usually long and strong, rarely short and weak. Female with each half of sternite 8 bluntly rounded apically (Fig. 37) .... ***Cordilura*** (***Cordilura*** Fallén), in part
see couplet 14



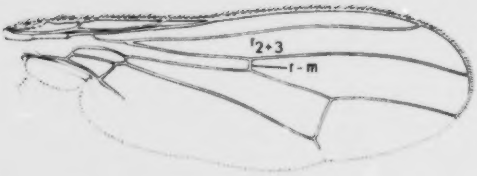
25 Ernoneura argus ♂



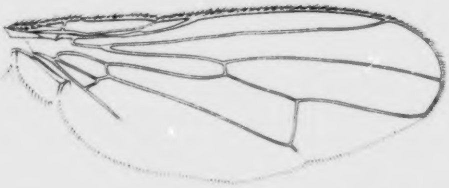
26 Cordilura (Scoliaphleps) ustulata ♂



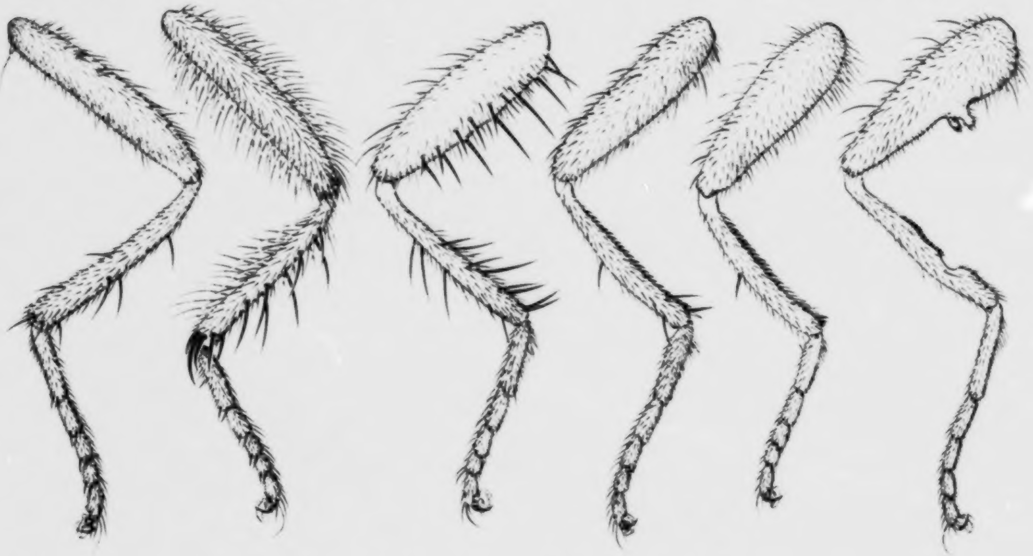
27 Cordilura (Achaetella) varipes ♂



28 Cordilura (Cordilurina) pleuritica ♂



29 Pogonota sahlbergi ♀



30 Scathophaga obscura ♂

31 Scathophaga intermedia ♂

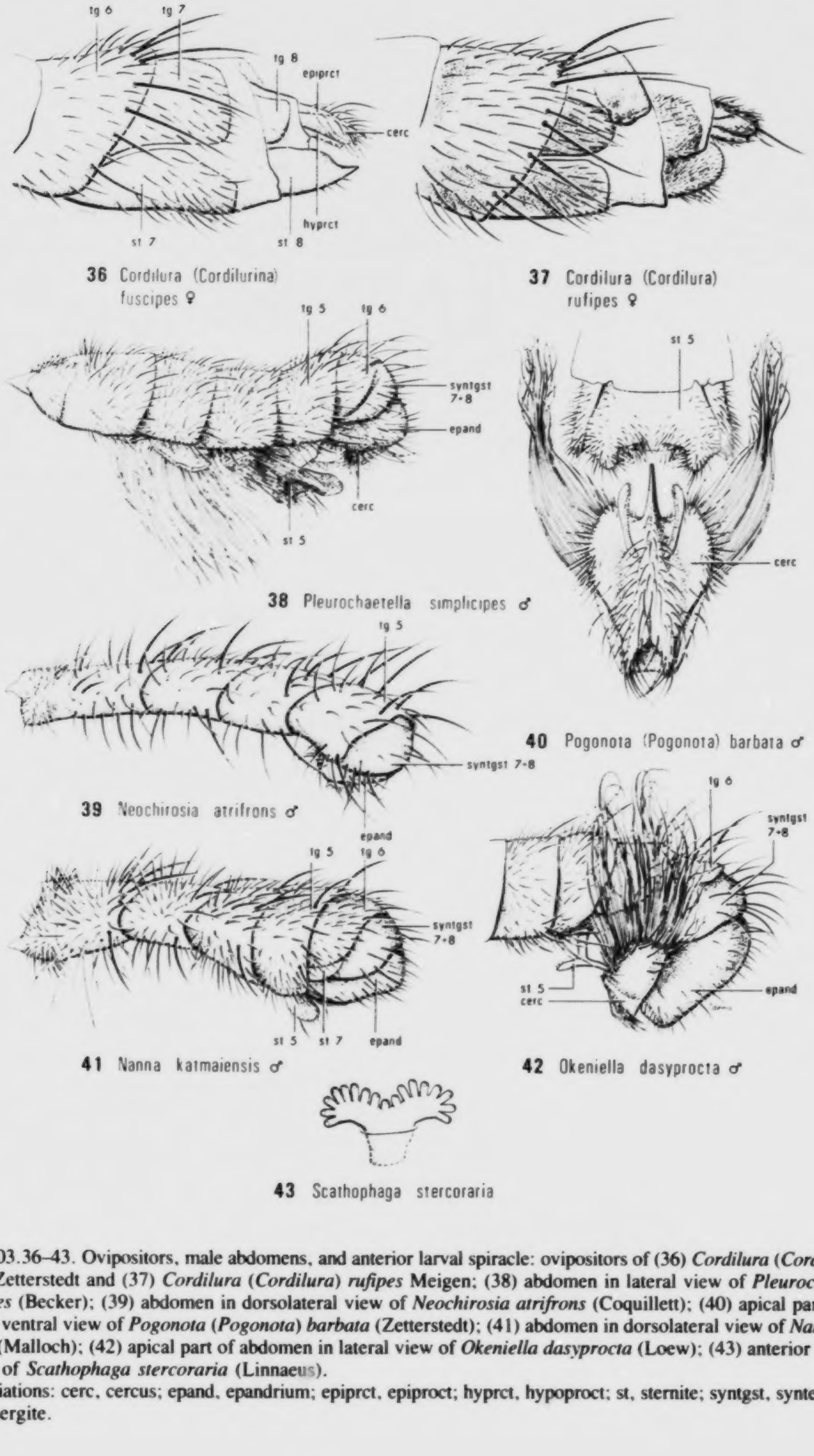
32 Norellisoma spinimanum ♂

33 Acanthocnema albibarba ♂

34 Microprosopa haemorrhoidalis ♂

35 Cosmetopus longus ♂

Figs. 103.25–35. Wings and legs: wings of (25) *Ernoneura argus* (Zetterstedt), (26) *Cordilura (Scoliaphleps) ustulata* Zetterstedt, (27) *Cordilura (Achaetella) varipes* (Walker), (28) *Cordilura (Cordilurina) pleuritica* Loew, and (29) *Pogonota sahlbergi* (Becker); left hindleg of (30) *Scathophaga obscura* (Fallén), and (31) *Scathophaga intermedia* Walker; left foreleg of (32) *Norellisoma spinimanum* (Fallén), (33) *Acanthocnema albibarba* (Loew), (34) *Microprosopa haemorrhoidalis* (Meigen), and (35) *Cosmetopus longus* (Walker).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syntgst 7+8
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cerc
epand

36 Cordilura (Cordilurina) fuscipes ♀

37 Cordilura (Cordilura) rufipes ♀

38 Pleurochaetella simplicipes ♂

39 Neochirosia atrifrons ♂

40 Pogonota (Pogonota) barbata ♂

41 Nanna katmaiensis ♂

42 Okeniella dasyprocta ♂

43 Scathophaga stercoraria

Figs. 103.36–43. Ovipositors, male abdomens, and anterior larval spiracle: ovipositors of (36) *Cordilura* (*Cordilurina*) *fuscipes* Zetterstedt and (37) *Cordilura* (*Cordilura*) *rufipes* Meigen; (38) abdomen in lateral view of *Pleurochaetella simplicipes* (Becker); (39) abdomen in dorsolateral view of *Neochirosia atrifrons* (Coquillett); (40) apical part of abdomen in ventral view of *Pogonota* (*Pogonota*) *barbata* (Zetterstedt); (41) abdomen in dorsolateral view of *Nanna katmaiensis* (Malloch); (42) apical part of abdomen in lateral view of *Okeniella dasyprocta* (Loew); (43) anterior spiracle of larvae of *Scathophaga stercoraria* (Linnaeus).

Abbreviations: cerc, cercus; epand, epandrium; epiprct, epiproct; hyprct, hypoproct; st, sternite; syntgst, syntergosternite; tg, tergite.

16. Ocellar bristles, and most fronto-orbital bristles, not longer than diameter of an ocellus (Fig. 11). Scutellum flat above; bristles short and spinose, with the longer pair shorter than length of scutellum .... ***Hydromyza*** Fallén

1 sp., *confluens* Loew; widespread

Ocellar and fronto-orbital bristles many times as long as diameter of an ocellus (Figs. 5, 8). Scutellum gently convex above; the longest bristles longer than scutellum 17

17. Fore femur and fore tibia each with an anteroventral and a posteroventral row of long stout black bristles (Fig. 32) .... ***Norellisoma*** Wahlgren

1 sp., *spinimanum* (Fallén); widespread

Fore femur and fore tibia each with at most one row of bristles beneath, never with a double row of long stout black bristles (Figs. 33–35) 18

18. Arista not longer than maximum length of first flagellomere measured on its dorsolateral surface (Fig. 17). A_1 incomplete, ending a short distance before wing margin .... ***Acerocnema*** Becker

2 spp.; widespread

Arista at least 1.25 times as long as first flagellomere. A_1 complete or incomplete 19

19. Scutellum with one pair of strong bristles 20

Scutellum with two pairs of strong subequal bristles 22

20. Aristal hairs several times as long as basal diameter of arista .... ***Megaphthalma*** Becker

1 sp., *pallida* (Fallén); widespread

Aristal hairs not longer than basal diameter of arista .... ***Bucephalina*** Malloch 21

21. Posterior part of head produced strongly downward; width of gena posteriorly more than one-half height of eye. Hairs of katepisternum, coxae, and ventral surfaces of femora almost all black .... ***Bucephalina*** (***Bucephalina*** Malloch)

2 spp.; eastern

Posterior part of head produced only very slightly downward; width of gena posteriorly at most one-half height of eye. Hairs of katepisternum, coxae, and ventral surfaces of femora almost all pale .... ***Bucephalina*** (***Neogimnomera*** Malloch)

1 sp., *amans* (Cresson); western

22. Anterior margin of postpronotum with many short erect black setulae (Fig. 22) .... ***Gimnomera*** Rondani, in part

4 spp.; widespread

Anterior margin of postpronotum without erect black setulae 23

23. R_1 setose dorsally on apical half .... ***Gimnomera*** Rondani, in part

see couplet 22

R_1 bare above 24

24. Apex of fore tibia with a short stout erect black midventral spine (Fig. 33) .... ***Acanthocnema*** Becker 25

Apex of fore tibia without an erect ventral spine 26

25. Anterior orbital bristle proclinate; the other two orbital bristles more or less lateroclinate but not extending beyond the most lateral part of the eye. Yellowish brown or brown species with face and gena yellow or whitish yellow .... ***Acanthocnema*** (***Acanthocnema*** Becker)

2 spp.; widespread

All orbital bristles lateroclinate, the longest usually extending beyond the most lateral part of the eye. Dark bluish gray species with face and gena gray; gena sometimes densely silver pruinose .... ***Acanthocnema*** (***Clinoceroides*** Hendel)

1 sp., *capillata* (Loew); eastern

26. Cells bm and cup bare, without microtrichia (as in Fig. 27). Palpus with a single distinct black apical bristle .... ***Americina*** Malloch, in part

1 sp., *adusta* (Loew); eastern

Wing membrane entirely trichose. Palpus without a single distinct apical bristle 27

27. Underside of fore tibia with many very short blunt black setulae (Figs. 34, 35). Arista bare 28

Underside of fore tibia haired, the vestiture not differing from that of other tibial surfaces. Arista bare, pubescent, or plumose 42

28. Male 29

Female 35

29. Cerci very large, fused, in the form of a broad plate with a sharp median keel lying below the epandrium (Fig. 40) .... **Pogonota** Zetterstedt 30

Cerci usually very small, if large not fused and without median keel 31

30. Head with long dense beard (Fig. 5). Cercus with long dense lateral fringe (Fig. 40) .... **Pogonota** (**Pogonota** Zetterstedt), in part

3 spp.; boreal; Malloch 1931 (as *Okenina* Malloch)

Head without beard. Cercus without lateral fringe .. **Pogonota** (**Lasioscelus** Becker), in part

2 spp.; Arctic

31. Cerci very large, divergent, with long lateral fringe that extends far above dorsal surface of abdomen (Fig. 42) .... **Okeniella** Hendel, in part

1 sp., *dasyprocta* (Loew); low Arctic

Cerci small, not divergent, without hairs that extend above dorsal surface of abdomen 32

32. Fore femur with forked tubercle below; opposing surface of fore tibia with a distinct excavation (Fig. 35) .... **Cosmetopus** Becker, in part

1 sp., *longus* (Walker); boreal

Fore femur without tubercle; fore tibia without excavation 33

33. Lateral margins of abdominal sternites 3 and 4 with many long strong yellow hairs that converge beneath abdomen (Fig. 38) .... **Pleurochaetella** Vockeroth, in part

1 sp., *simplicipes* (Becker); Arctic

Abdominal sternites 3 and 4 with only short weak hairs 34

34. Anterior supra-alar bristle absent. Prosternum haired. Palpus about as long as proboscis, curved, enlarged toward apex, and with rather strong black lateral bristles .... **Brooksiella** Vockeroth, in part

1 sp., *varicornis* (Curran); boreal, western

Anterior supra-alar bristle short but distinct. Prosternum bare. Palpus about half as long as proboscis, without outstanding bristles 41

35. Fore femur with short black erect setulae on ventral surface (Fig. 34) 36

Fore femur without black setulae below 39

36. Apex of M curved slightly forward (Fig. 29) .... **Pogonota** Zetterstedt 37

Apex of M curved slightly backward (as in Fig. 25) 38

37. Anterior postsutural intra-alar bristle very weak, not longer than posterior notopleural bristle .... **Pogonota** (**Pogonota** Zetterstedt), in part

see couplet 30

Anterior postsutural intra-alar bristle strong, twice as long as posterior notopleural bristle .... **Pogonota** (**Lasioscelus** Becker), in part

see couplet 30

38. Anterior supra-alar bristle subequal to posterior notopleural bristle. Apical third of A_1 very weak, the vein sometimes not reaching wing margin .... **Okeniella** Hendel, in part

see couplet 31

Anterior supra-alar bristle about half as long as posterior notopleural bristle. A_1 at most slightly weakened very near wing margin .... **Pleurochaetella** Vockeroth, in part

see couplet 33

39. Anterior supra-alar bristle absent. Prosternum haired .... **Brooksiella** Vockeroth, in part

see couplet 34

Anterior supra-alar bristle short but distinct. Prosternum bare 40

40. Hind tibia without posterodorsal bristle. First flagellomere yellow at base .... **Cosmetopus** Becker, in part

see couplet 32

Hind tibia with at least one posterodorsal bristle. First flagellomere entirely black 41

41. Femora mostly or entirely black, gray pruinose. Scutum entirely pruinose. Anepimeron with a few fine hairs or bare .... ***Allomyella*** Malloch
6 spp.; Arctic

Femora entirely bright yellow or, if dark reddish brown, then scutum with shining black stripes. Anepimeron bare .... ***Microprosopa*** Becker
6 spp.; widespread

42. Gena more than half height of eye (Fig. 8). Proepimeron bare or with at most one weak bristle .... ***Staegeria*** Rondani
1 sp., unnamed; boreal

Gena two-fifths height of eye or less. Proepimeron with a bristle and a few hairs 43

43. Anterior supra-alar bristle absent 44

Anterior supra-alar bristle present, usually long 45

44. Postpronotum, anepisternum, and anepimeron with shining black areas. Presutural acrostichal hairs in two regular rows .... ***Cordylurella*** Malloch
2 spp.; eastern

Thorax gray or brown, entirely pruinose. Presutural acrostichal hairs in three or more irregular rows .... ***Spaziphora*** Rondani
1 sp., *cincta* (Loew); widespread

45. Abdominal tergites black, slightly pruinose dorsally, strongly shining laterally .... ***Huckettia*** Vockeroth
1 sp., *nearctica* Vockeroth; Arctic

Abdominal tergites either mostly yellow or entirely pruinose 46

46. Anepimeron haired. Arista pubescent .... ***Megaphthalmoides*** Ringdahl
1 sp., *unilineatus* (Zetterstedt); widespread

Anepimeron bare. Arista bare or plumose 47

47. Arista plumose .... ***Scathophaga*** Meigen, in part
see couplet 5

Arista bare 48

48. First flagellomere with upper apical angle rounded (Fig. 18) .... ***Trichopalpus*** Rondani
1 sp., *obscurella* (Zetterstedt); boreal

First flagellomere with upper apical angle acute (Fig. 19) .... ***Chaetosa*** (***Opsiomyia*** Coquillett)
2 spp.; widespread

49. Scutellum with two pairs of strong subequal bristles 50

Scutellum with one pair of bristles 55

50. R_1 setose above on apical half .... ***Orthacheta*** Becker
3 spp.; widespread

R_1 bare above 51

51. Katepisternum with three strong bristles .... ***Gonarcticus*** Becker, in part
2 spp.; Arctic, boreal

Katepisternum with two bristles, the anterior one sometimes weak 52

52. Katepisternal bristles in a nearly vertical row, subequal 53

Katepisternal bristles in a nearly horizontal row, the anterior one much weaker 54

53. Hind tibia with posteroventral apical bristle not more than one-fourth as long as anteroventral apical bristle. Female terminalia not compressed .... ***Gonarcticus*** Becker, in part
see couplet 51

Hind tibia with posteroventral apical bristle subequal to anteroventral apical bristle. Female terminalia strongly compressed .... ***Gonatherus*** Rondani
1 sp., *planiceps* (Fallén); boreal

54. Two presutural intra-alar and two postsutural intra-alar bristles present. Wing membrane entirely trichose .... ***Chaetosa*** (***Chaetosa*** Coquillett)
2 spp.; widespread; Malloch 1931

Presutural and postsutural intra-alar bristles absent. Cells bm and cup bare, without microtrichia .... ***Americina*** Malloch, in part
see couplet 26

55. R₁ setose above on apical half .... ***Neorthacheta*** Vockeroth
1 sp., *dissimilis* (Malloch); eastern

R₁ bare above .... ***Nanna*** Becker, in part
9 spp.; widespread

56. Katepisternum with one bristle .... ***Parallelomma*** Becker
1 sp., *vittatum* (Meigen); widespread

Katepisternum with two or three bristles 57

57. Frons with one proclinate and one reclinate orbital bristle (Figs. 9, 10, 12, 13). Male with one pregenital sclerite visible between tergite 5 and epandrium (Fig. 39) 58

Frons with one proclinate and two reclinate orbital bristles (as in Figs. 6, 7). Male with two pregenital sclerites visible between tergite 5 and epandrium (Fig. 41) 63

58. Katepisternum with two bristles, the anterior sometimes much weaker than the posterior 59

Katepisternum with three moderately strong bristles 62

59. Katepisternal bristles subequal 60

Anterior katepisternal bristle much weaker than posterior bristle 61

60. Face strongly receding below; lower half of postcranium with rather long pale hairs (Fig. 9). Anterior presutural intra-alar bristle absent; anterior supra-alar bristle longer than posterior notopleural bristle .... ***Hexamitocera*** Becker
1 sp., *loxocerata* (Fallén); northwestern

Face only slightly receding below; lower half of postcranium with very short mixed pale and dark hairs (Fig. 10). Anterior presutural intra-alar bristle present; anterior supra-alar bristle, if present, much shorter than posterior notopleural bristle ... ***Peratomyia*** Vockeroth
1 sp., *vittata* (Coquillett); central and western

61. Frons with two strong frontal bristles. Body yellow .... ***Synchysa*** Vockeroth
1 sp., *tricincta* (Loew); widespread

Frons with three or more strong frontal bristles. Body black ... ***Delina*** Robineau-Desvoidy
1 sp., *nigrita* (Fallén); boreal

62. Anterior margin of frons, above base of antennae, with a deep triangular emargination (Fig. 12) .... ***Plethochaeta*** Coquillett
2 spp.; widespread

Anterior margin of frons, above base of antennae, with a shallow rounded emargination (Fig. 13) .... ***Neochirosia*** Malloch
3 spp.; widespread

63. R₁ setose above on apical one-third .... ***Dromogaster*** Vockeroth
1 sp., *incompta* Vockeroth; central and western

R₁ bare above .... ***Nanna*** Becker, in part
see couplet 55

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ANTHOMYIIDAE

104

H. C. HUCKETT

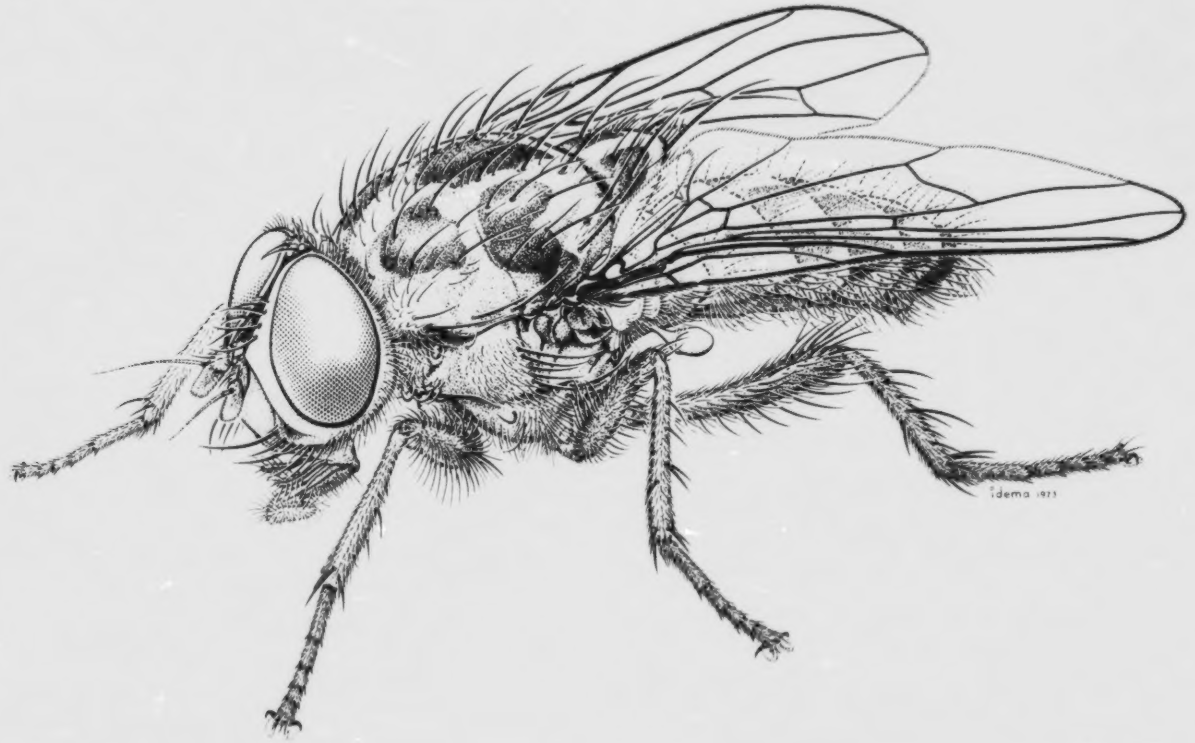


Fig. 104.1. Adult male of *Anthomyia pluvialis* (Linnaeus).

Small to moderately large muscid-like flies (Fig. 1), 2.0–12.0 mm long, usually drab yellow, brown, gray, or blackish, and nonmetallic. Wing sometimes dusky, rarely spotted. Legs yellowish to black.

Adult. Head: frequently holoptic in male (Fig. 4), usually broadly dichoptic in female (Fig. 2), but rarely narrowly so (Fig. 6). Frons with frontal, vertical, and ocellar bristles, and in dichoptic cases usually with orbital bristles; cruciate interfrontal setae present or absent; vibrissae present (Figs. 2–14). Eye bare to densely haired. Antenna pendant; first flagellomere subquadrate or oblong; arista bare to plumose. Proboscis slender (Fig. 15) to stout (Fig. 16), occasionally long and tubular (Fig. 17); palpus filiform, clavate, or spatulate.

Thorax: scutum (Figs. 18, 19) almost always with paired postsutural acrostichal bristles or setulae, and usually also with similar presutural acrostichal bristles; acrostichal setulae and hairs sometimes arranged in two series (four rows); one or two pairs of presutural dorsocentral bristles and one to four pairs of postsutural dorsocentral bristles usually present; one presutural intra-alar bristle and two postsutural intra-alar bristles usually present on each side; one presutural supra-alar and two or three postsutural supra-alar bristles also usually present; postalar callus with two postalar bristles; notopleuron always with two notopleural bristles. Postpronotal lobe with one or two postpronotal bristles. Scutellum (Figs. 18, 19, 23, 26) with one pair of apical and one pair of basal bristles, and usually with hairs on ventral surface. Proepisternum, anepimeron, meron, and prosternum usually without hairs, but occasionally haired; all these sclerites haired in certain species of *Eutrichota* Kowartz (=*Eremomyioides* Malloch) (Fig. 18); meron always without strong bristles; katepisternum (Figs. 19, 24, 25) with anterior and posterior bristles on upper border, sometimes with bristles arranged in an equilateral triangle, e.g. in *Chelisia elegans* Stein (Fig. 24).

Wing (Figs. 27–30) with C reaching to apex of M_1 and without widely spaced outstanding spinules on lower surface, except in Fucelliinae; lower surface finely setulose in some groups, e.g. *Botanophila* Lioy (Fig. 28); main veins, other than C, without hairs or setulae on upper and lower surfaces except occasionally on lower surface of basal nodes of R and

M. Cell r_{4+5} widely open at wing margin; A_1 traceable to wing margin except in *Acridomyia* Stackelberg (Fig. 30) and *Coenosopsia* Malloch. Lower calypter narrower than, subequal to, or longer than upper calypter.

Legs (Figs. 31–38) slender and bristly, frequently sexually dimorphic; those of male usually with more abundant, longer, and stronger hairs and bristles than those of female. Chaetotaxy of tibiae (Figs. 31–34) particularly important in classification and identification at all taxonomic levels. Tarsomere 1 of hind tarsus usually, if not always, with a prominent subbasal ventral bristle (Figs. 31–34); apical tarsomeres of fore tarsus sometimes distinctly swollen or dorsoventrally flattened, especially in female (Figs. 35–38).

Abdomen: usually cylindrical and rather conical (Fig. 1). Seven pairs of spiracles present in both sexes; first five pairs located in margins of tergites. Male with left one of sixth pair situated in membrane, but right one enclosed in margin of tergite 6; left one of seventh pair in left side of syntergosternite 7 + 8, and right one in right side of syntergosternite 7 + 8. Female with spiracles 6 and 7 often closely adjacent in tergite 6.

Male with sternite 5 bilobate posteriorly (Figs. 44–47). Tergite 6 (prebasal sclerite) small, usually bare (Figs. 48–51); sternite 6 narrow, strap-like, broadly overlapped by sternite 5. Tergites 7 and 8, and probably elements of sternites 7 and 8, fused to form a dorsal syntergosternite (basal sclerite) (Figs. 48–51). Epandrium small; surstylus articulated, usually long and slender or spatulate. Hypandrium small; aedeagus with simple basiphallus and more complex distiphallus; epiphallus small, lamellate; gonopod and paramere distinct (Figs. 50, 51). Cerci fused, rigid, and scutate or rostrate.

In female, ovipositor (Figs. 39–43) usually tubular, with long flexible intersegmental membranes. Tergites and sternites reduced or longitudinally subdivided; sternite 8 seldom strongly sclerotized. Cerci small, papillate.

Larva. Muscidiform (Fig. 52), slender, smooth except for cuticular granulations and patches of fine spicules, and subtruncate posteriorly with peripheral ring of distinct papillae. Cephalopharyngeal skeleton (Fig. 54) of generalized saprophagous form; mandible simple or dentate, separate, without accessory sclerites, and usually short and weakly curved; hypopharyngeal sclerite well-developed; parastomal bars usually present; tentoropharyngeal sclerite deeply grooved, with equal musculature dorsally and ventrally, and flaring caudally as paired dorsal and ventral cornua; each cornu with clear window-like subterminal lacuna. Anterior spiracle (Fig. 54) with few to many papillae. Posterior spiracles (Fig. 55) situated slightly dorsal of center of spiracular disc; each with three circular, short or long oval, or linear spiracular openings that radiate outward from a marginal ecdysial scar. Description after Roback (1951) and Hennig (1952).

Biology and behavior. The larvae are mostly phytophagous or saprophagous and live in stems, roots, flower heads, and foliage of decayed or living plants, some of which are important economically. Some are scavengers or coprophagists, living in droppings of animals and birds. Others are inquilines, commensals, or parasites, living in burrows of solitary bees and wasps, rodents, and land turtles. Still others are found on the seashore feeding on kelp, seaweed, and *Fucus* washed up by the sea, or in aquatic or semiaquatic media near freshwater ponds and streams.

Classification and distribution. Until recently the Anthomyiidae, commonly called root-maggot flies, were treated as a subfamily of the Muscidae (Huckett 1965*a*), and sometimes the Scathophagidae or dung flies were included with them (Huckett 1965*b*). Now, however, in line with recent advances in the classification of all muscoid flies, they are ranked as a separate family. The family is world wide in distribution, but it is best represented in the Temperate Zones, especially in the Holarctic region. Nearly 600 species belonging to 50–60 genera and subgenera are known in the Nearctic region. A similar number are known in the Palaearctic region. As in many groups of flies, there is a close affinity between the anthomyiid faunas of the Nearctic and Palaearctic regions. Over one-quarter of the Nearctic species have Holarctic distributions. Because so many of these species are associated with food crops, ornamentals, and common weeds, a fair number of them have been introduced into North America from Europe by humans. But many others, especially in Boreal and Arctic regions, dispersed to and from both regions without the help of people.

The classification followed in this treatment is essentially the same as was used in the treatment of the Muscidae of Northern Canada, Alaska, and Greenland (Huckett 1965*a*) and of the Anthomyiidae of California (Huckett 1971). It is admittedly somewhat at variance with that of Hennig in his treatment of the Palaearctic fauna (Hennig 1976), which was still incomplete when this section was prepared in 1972. A treatment of Nearctic Anthomyiidae by Griffiths, now in progress (Griffiths 1982, 1983, 1984*a*, 1984*b*) will probably incorporate needed improvements in the classification of the family in North America. Those working on the family should consult both these treatments.

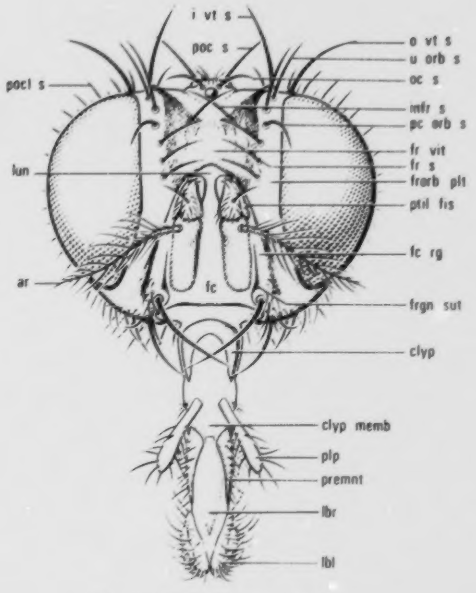
The only fossil referred to the Anthomyiidae is from Florissant, Colorado (Cockerell 1913).

Key to genera

1. A_1 sharply abbreviated far before wing margin (Fig. 30). Scutellum without hairs on ventral surface 2

A_1 traceable to wing margin (Fig. 29). Scutellum usually with hairs on ventral surface (Figs. 19, 23, 26) 3

2. Palpus absent. Larvae parasitic on grasshoppers . . . . ***Acridomyia*** Stackelberg
2 spp.; central and eastern North America; Snyder 1940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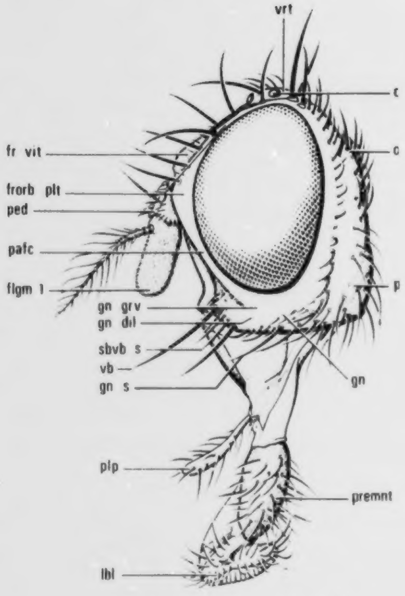
2 Hylemya alcathoe ♀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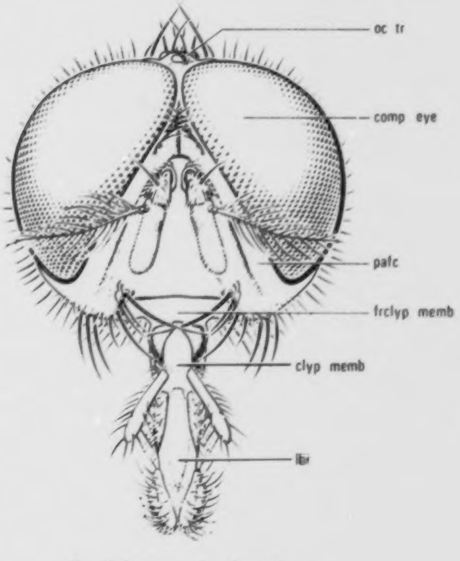
3 Hylemya alcathoe ♀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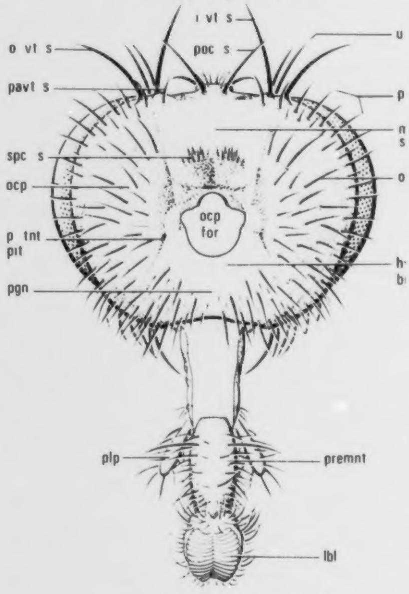
4 Hylemya alcathoe ♂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5 Hylemya alcathoe ♀

Figs. 104.2-5. Head of *Hylemya alcathoe* (Walker): (2) anterior, (3) left lateral, and (5) posterior views of female; (4) anterior view of male. Note dichoptic condition of female (2) and holoptic condition of male (4).

Abreviations: ar, arista; clyp, clypeus; clyp memb, clypeolabral membrane; comp eye, compound eye; fc, face; fc rg, facial ridge; flgm, flagellomere; frclyp memb, frontoclypeal membrane; frgn sut, frontogenal suture; frorb plt, fronto-orbital plate; fr s, frontal seta; fr vit, frontal vitta; gn, gena; gn dil, genal dilation; gn grv, genal groove; gn s, genal seta; hyps brg, hypostomal bridge; infr s, interfrontal seta; i vt s, inner vertical seta; lbl, labella; lbr, labrum; lun, lunule; m ocp scl, median occipital sclerite; oc, ocellus; ocp, occiput; ocp for, occipital foramen; ocp s, occipital seta; oc s, ocellar seta; oc tr, ocellar triangle; o vt s, outer vertical seta; pafc, parafacial; pavt s, paravertical seta; pc orb s, proclinate orbital seta; ped, pedicel; pgn, postgena; plp, palpus; pocl s, postocular seta; poc s, postocellar seta; premnt, prementum; ptil fis, ptilinal fissure; p tnt pit, posterior tentorial pit; sbvb s, subvibrissal setula; spc s, supracervical seta; u orb s, upper orbital seta; vb, vibrissa; vrt, vertex.

Palpus present (Figs. 2–4). Larvae not parasitic .... ***Coenosopsia*** Malloch

1 sp., *prima* Malloch; Florida and Texas

3. C with widely spaced coarse setae on lower surface distal to subcostal break. Scutellum usually without hairs on ventral surface .... FUCELLIINAE....4

C without widely spaced coarse setae on lower surface distal to subcostal break (but sometimes with closely set fine setulae present, e.g. in *Botanophila* Lioy (Fig. 28), *Chelisia* Rondani, and some *Pegomya* Robineau-Desvoidy). Scutellum usually with hairs present on ventral surface (as in Figs. 19, 23, 26), except in some species of Myopinini .... ANTHOMYIINAE....5

4. Thorax with two pairs of presutural dorsocentral bristles (as in Fig. 18) .... ***Fucellia*** Robineau-Desvoidy

19 spp.; widespread; Huckett 1965*a* and 1971, Hennig 1966

Thorax with one pair of presutural dorsocentral bristles .... ***Circia*** Malloch

1 sp., *tinctipennis* Malloch; Alaska, Alberta

5. Katepisternal bristles arranged in a nearly equilateral triangle (Fig. 24). Wing in male pale and usually narrow at base, usually darkened on apical half .... CHELISIINI.... ***Chelisia*** Rondani

1 sp., *elegans* Stein; California

Katepisternal bristles not arranged in an equilateral triangle (Figs. 19, 25). Wing not as above 6

6. Scutellum usually without hairs on ventral surface; if haired, frons in male and female similarly broad and similarly bristled; width of frons at vertex exceeding distance between anteriormost pair of dorsocentral bristles .... MYOPININI....7

Scutellum usually with hairs on ventral surface (as in Figs. 19, 23, 26); if hairless, frons in male and female usually dissimilar in breadth and bristling, but if similar, then width of frons at vertex usually not more than distance between anteriormost pair of dorsocentral bristles .... ANTHOMYIINI....10

7. Hind tibia with robust apical posteroventral bristle .... ***Chirosia*** Rondani

2 spp.; widespread; Huckett 1971

Hind tibia without apical posteroventral bristle 8

8. Antenna and face short; first flagellomere scarcely longer than wide; face shorter than length of frons; cheek narrower than width of proboscis, when viewed laterally .... ***Chiastocheta*** Pokorny

2 spp.; western North America

Antenna and face long; first flagellomere much longer than wide; face longer than length of frons; cheek broader than width of proboscis, when viewed laterally 9

9. Parafacial narrow, ventrally nearly linear in profile. Abdomen in male conical; processes of sternite 5 shining and blade-like as in *Paraprosalpia* Villeneuve (Fig. 47) .... ***Pseudochirosia*** Ringdahl

2 spp.; northern North America; Ringdahl 1959, Huckett 1965*a*

Parafacial broad, not so notably narrowed ventrally. Abdomen in male short and stubby, much swollen caudally; processes of sternite 5 not shining and blade-like .... ***Myopina*** Robineau-Desvoidy

3 spp.; northern North America; Ringdahl 1959, Huckett 1965*a*

10. Middle of proepisternum with hairs (Fig. 19) 11

Middle of proepisternum without hairs 14

11. Anepimeron, meron, katepimeron, and prosternum simultaneously with hairs (Fig. 19) .... ***Eremomyioides*** Malloch

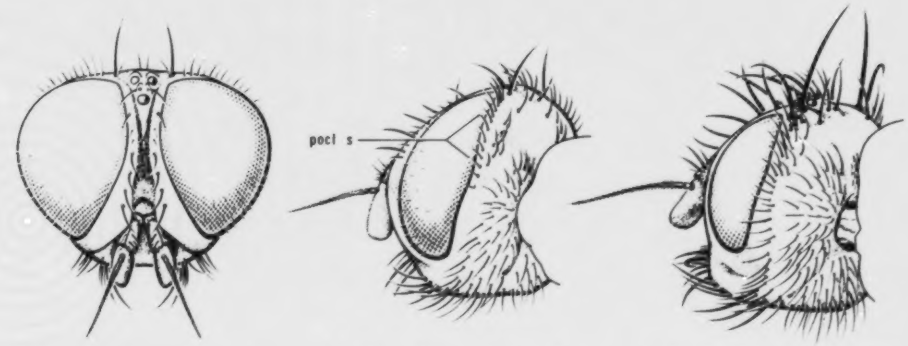
6 spp.; widespread; Huckett 1944, Griffiths 1984*b* (as *Eutrichota*)

Anepimeron, meron, katepimeron, and prosternum not simultaneously with hairs; one or more of these sclerites bare 12

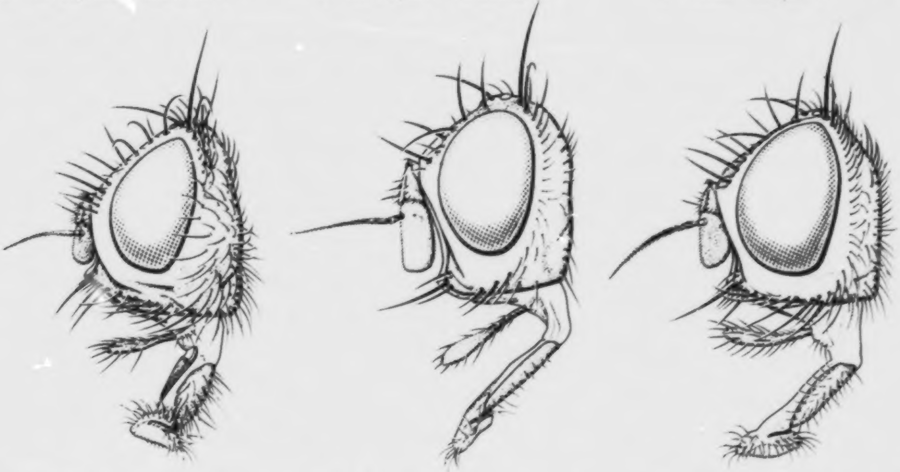
12. Thorax pale gray; scutum with contrasting large dark spot and markings (Fig. 1) .... ***Anthomyia*** Meigen

2 spp.; widespread; Huckett 1965*a*, 1971

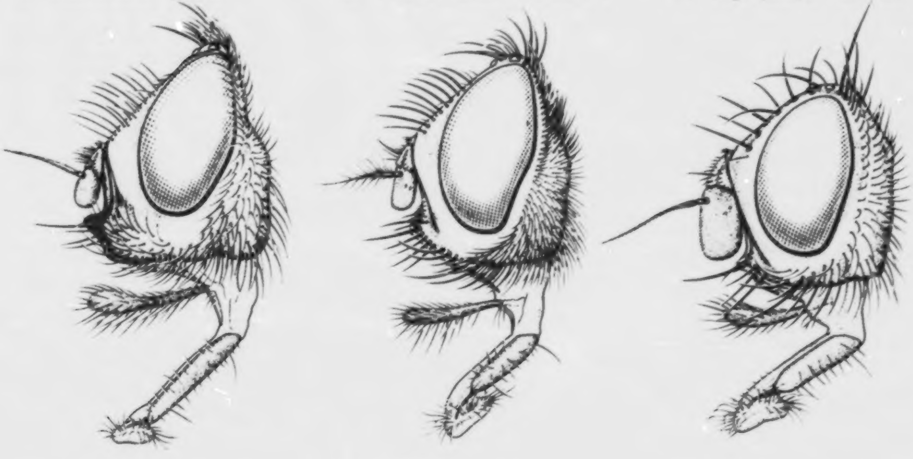
Thorax not pale gray; scutum marked other than above 13



6 Leucophora maculata ♀ 7 Leucophora maculata ♀ 8 Delia antiqua ♀



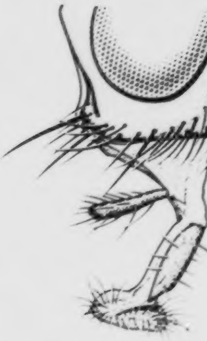
9 Chiastocheta glauca ♀ 10 Pseudochirosia fractiseta ♀ 11 Pegohylemyia trivittata ♀



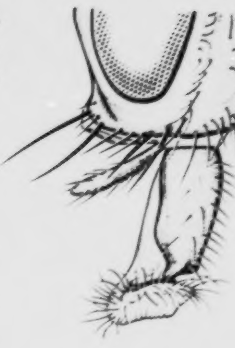
12 Egle muscaria ♂ 13 Hydrophoria divisa ♂ 14 Lasiomma anthracina ♀

Figs. 104.6–14. Heads: (6) anterior and (7) left posterolateral views of *Leucophora maculata* (Stein); (8) left posterolateral view of *Delia antiqua* (Meigen); left lateral views of (9) *Chiastocheta glauca* (Coquillett), (10) *Pseudochirosia fractiseta* (Stein), (11) *Pegohylemyia trivittata* (Stein), (12) *Egle muscaria* (Fabricius), (13) *Hydrophoria divisa* (Meigen), and (14) *Lasiomma anthracina* (Czerny) (*continued*).

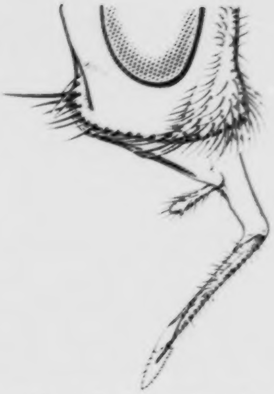
Abbreviation: pocl s, postocular setae.



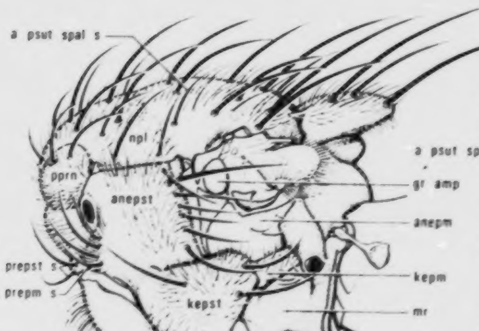
15 Phorbia sp. ♀



16 Pycnoglossa flavipennis ♀



17 Proboscimyia brevis ♀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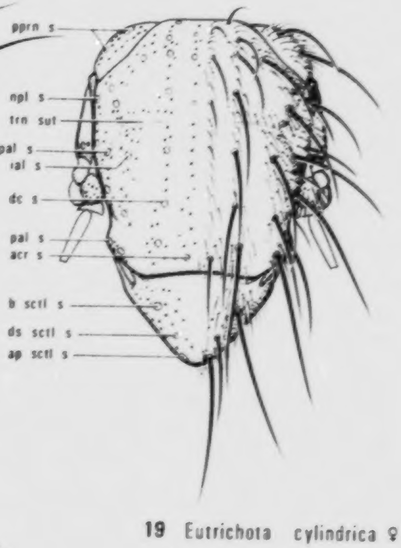
18 Eutrichota cylindrica ♀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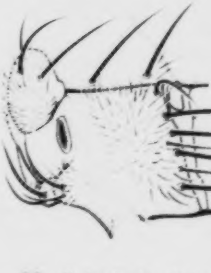
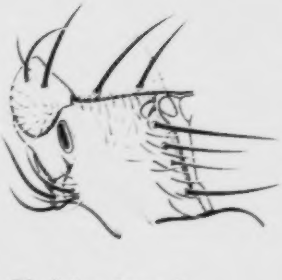
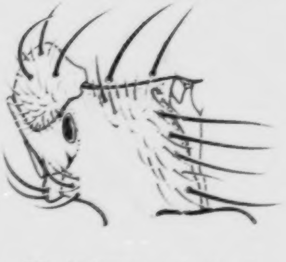
19 Eutrichota cylindrica ♀



20 Hydrophoria divisa ♀



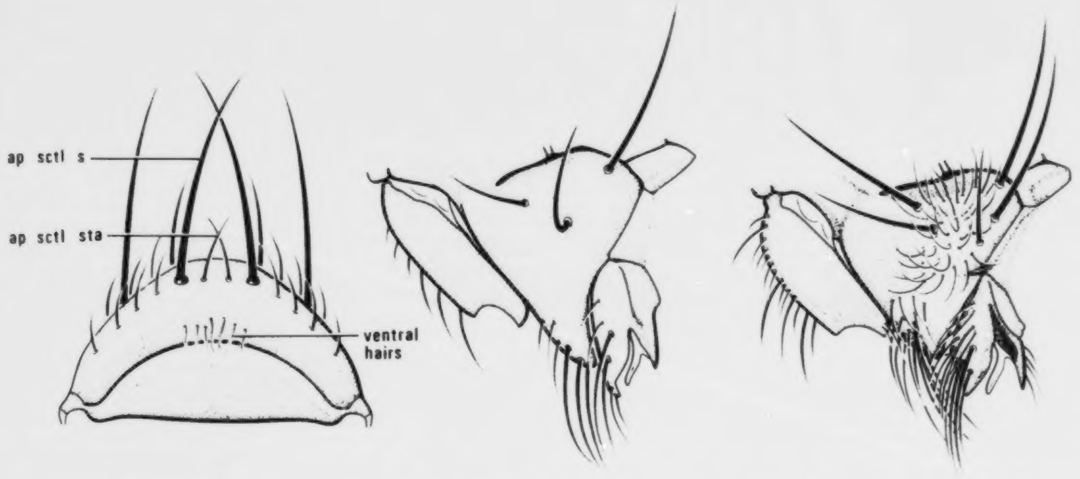
21 Delia platura ♀



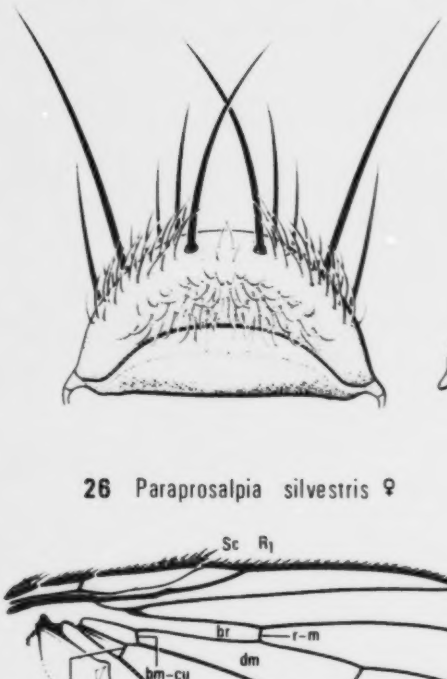
22 Lasiomma anthracina ♀

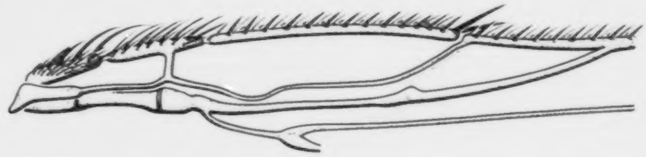
Figs. 104.15–22. Heads (*concluded*) and thoraces: proboscis and lower portion of head, left lateral views, of (15) *Phorbia* sp., (16) *Pycnoglossa flavipennis* (Fallén), and (17) *Proboscimyia brevis* Huckett; (18) dorsal and (19) left lateral views of thorax showing chaetotaxy of *Eutrichota cylindrica* (Stein); left anepisternum and adjoining areas of (20) *Hydrophoria divisa* (Meigen), (21) *Delia platura* (Meigen), and (22) *Lasiomma anthracina* (Czerny) (*continued*).

Abbreviations: acr s, acrostichal seta; anepm, anepimeron; anepst, anepisternum; ap sctl s, apical scutellar seta; a psut spal s, anterior postsutural supra-alar (prealar) seta; b sctl s, basal scutellar seta; cx, coxa; dc s, dorsocentral seta; ds sctl s, discal scutellar seta; gr amp, greater ampulla; ial s, intra-alar seta; kepm, katepimeron; kepst, katepisternum; mr, meron; npl, notopleuron; npl s, notopleural seta; pal s, postalar seta; pprn, postpronotum; pprn s, postpronotal seta; prepm s, proepimeral seta; prepst s, proepisternal seta; trn sut, transverse suture.

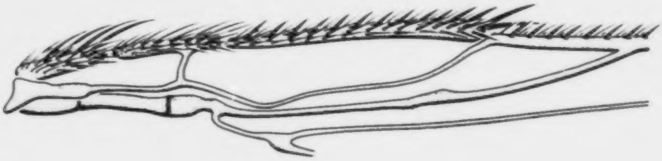


23 Pseudonupedia intersecta ♀ **24** Chelisia elegans ♂ **25** Hydrophoria flavohalterata ♀



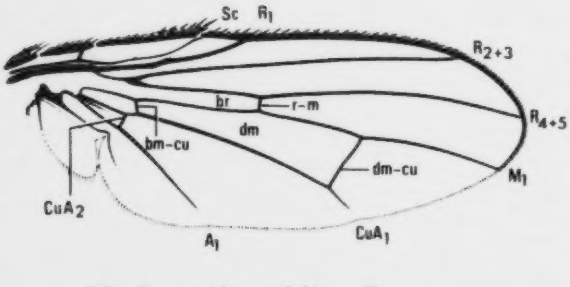


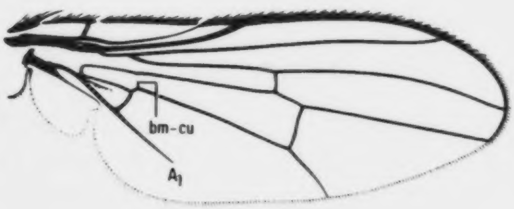
27 Pegohylemyia fugax ♀



26 Paraprosalpia silvestris ♀

28 Botanophila spinidens ♀





29 Botanophila spinidens ♀

30 Acridomyia canadensis ♂

Figs. 104.23–30. Thoraces (*concluded*) and wings: apex of scutellum, posteroventral views, of (23) *Pseudonupedia intersecta* (Meigen) and (26) *Paraprosalpia silvestris* (Fallén); chaetotaxy of mesothoracic katepisternum, left lateral views, of (24) *Chelisia elegans* Stein and (25) *Hydrophoria flavohalterata* Malloch; subcostal area of left wing, ventral views, of (27) *Pegohylemyia fugax* (Meigen) and (28) *Botanophila spinidens* (Malloch); right wing, dorsal views, of (29) *Botanophila spinidens* and (30) *Acridomyia canadensis* Snyder.

Abbreviations: ap sctl s, apical scutellar seta; ap sctl sta, apical scutellar setula.

13. Hind tibia with two posterodorsal bristles (as in Fig. 33) and without apical posteroventral bristle .... ***Paregle*** Schnabl, in part

5 spp., but only *aestiva* (Meigen), which Hennig (1966–1967) treated as *Nupedia aestiva* (Meigen), keys here; widespread; Huckett 1965*a*

Hind tibia with three or more posterodorsal bristles (as in Fig. 34) and with apical posteroventral bristle .... ***Crinurina*** Karl

2 spp.; widespread in north; Huckett 1965*a*

14. Katepimeron with hairs (as in Fig. 18) 15

Katepimeron without hairs 16

15. Prosternum with marginal hairs. Abdomen with tridentate marks .... ***Calythea*** Schnabl & Dziedzicki

3 spp.; widespread; Ackland 1968, Huckett 1971

Prosternum without hairs. Abdomen without tridentate marks .... ***Hydrophoria*** Robineau-Desvoidy, in part

35 spp.; widespread; Huckett 1965*a*

16. Thorax with four pairs of postsutural dorsocentral bristles 17

Thorax with three pairs of postsutural dorsocentral bristles (as in Fig. 19) 18

17. Proboscis slender; lower margin of face protruded forward (Fig. 12). Mid tibia without anteroventral bristle near middle .... ***Egle*** Robineau-Desvoidy, in part

10 spp.; widespread; Huckett 1965*a*

Proboscis not slender; lower margin of face not protruded (as in Fig. 13). Mid tibia with a strong anteroventral bristle near middle .... ***Macrophorbia*** Malloch

1 sp., *houghi* Malloch; eastern

18. Lower calypter distinctly extended beyond upper one 19

Lower calypter not distinctly extended beyond upper one 24

19. Anepimeron with bristle on dorsal margin below wing .... ***Emmesomyia*** Malloch

4 spp.; U.S.A., southern Canada; Griffiths 1984*a*

Anepimeron without bristles, rarely with hairs 20

20. Fore and hind tibiae (Fig. 32) each with one long conspicuous dorsal bristle beyond midpoint, exclusive of apical bristles .... ***Anthomyiella*** Malloch

1 sp., *pratincola* (Panzer); widespread

Fore tibia without strong dorsal bristle; hind tibia with more than one conspicuous dorsal or posterodorsal bristle (Figs. 33, 34) 21

21. Hind tibia with two posterodorsal bristles (Fig. 33); mid tibia without anteroventral bristle near middle 22

Hind tibia usually with three posterodorsal bristles (Fig. 34); if only two on hind tibia, mid tibia with anteroventral bristle near middle 23

22. Arista plumose (as in Figs. 2–4, 13) .... ***Hydrophoria*** Robineau-Desvoidy, in part

see couplet 15

Arista not plumose (as in Figs. 7–12) .... ***Pegomya*** Robineau-Desvoidy, in part

119 spp.; widespread, leaf miners; Huckett 1965*a*, 1971; Griffiths 1982, 1983, 1984

23. Lower margin of face distinctly protruded to level of lower margin of frons (as in Fig. 12) .... ***Adia*** Robineau-Desvoidy, in part

as *Paregle* Schnabl; see couplet 13

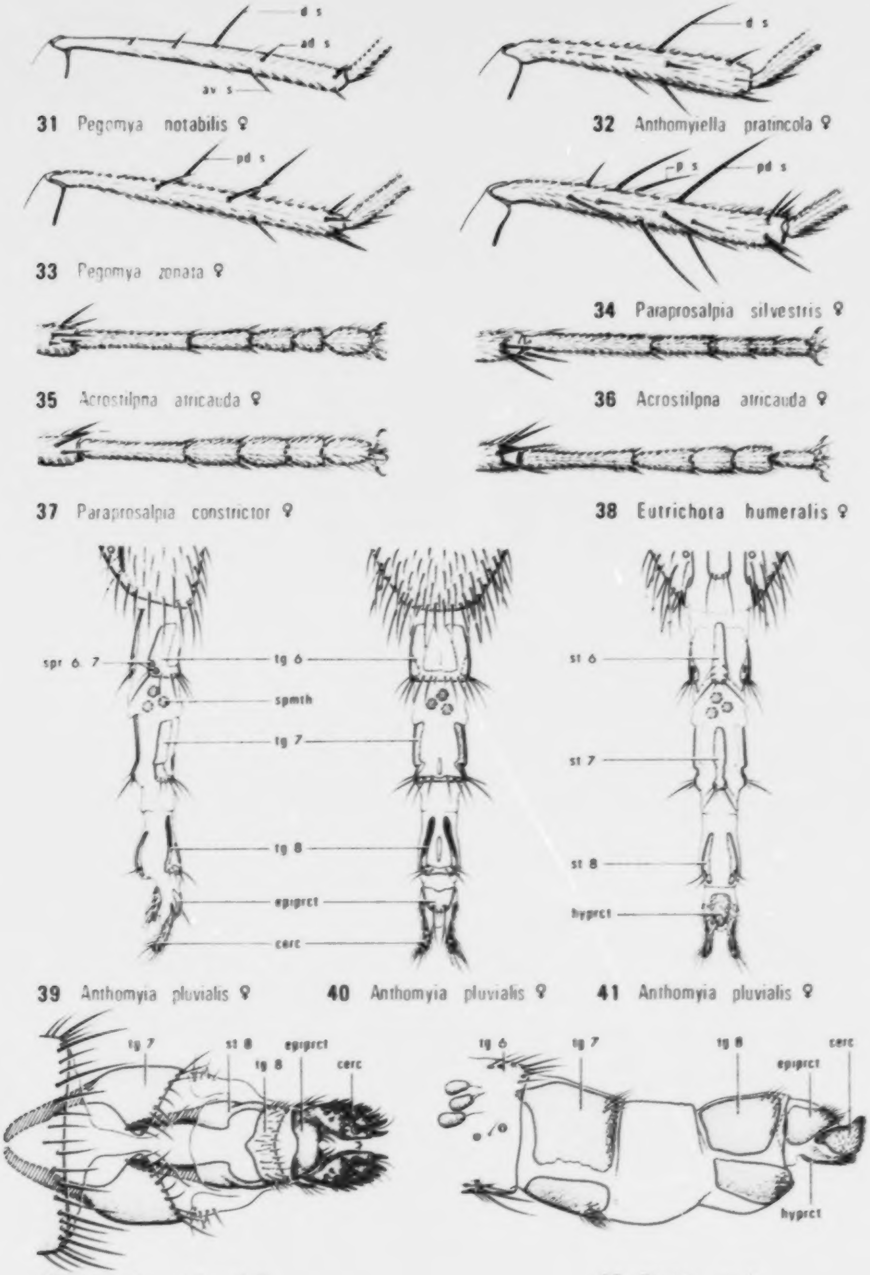
Lower margin of face not protruded to level of lower margin of frons (Fig. 13) .... ***Hydrophoria*** Robineau-Desvoidy, in part

see couplet 15

24. Head, thorax, and abdomen whitish gray; scutum with three contrasting stripes; abdomen with black middorsal stripe and transverse incisures. Cruciate interfrontal setae absent in both sexes .... ***Eustalomyia*** Kowarz

3 spp.; widespread; Huckett 1965*a*, 1971

Head, thorax, and abdomen usually other than above; if these whitish gray, cruciate interfrontal setae present (as in Fig. 2) 25



31 Pegomya notabilis ♀
32 Anthomyiella pratincola ♀
33 Pegomya zonata ♀
34 Paraprosalpia silvestris ♀
35 Acrostilpna atricauda ♀
36 Acrostilpna atricauda ♀
37 Paraprosalpia constrictor ♀
38 Eutrichota humeralis ♀
39 Anthomyia pluvialis ♀
40 Anthomyia pluvialis ♀
41 Anthomyia pluvialis ♀
42 Leucophora johnsoni ♀
43 Phorbia sp. ♀

Figs. 104.31–43. Legs and female terminalia: left hind tibia, anterodorsal views, of (31) *Pegomya notabilis* (Zetterstedt), (32) *Anthomyiella pratincola* (Panzer), (33) *Pegomya zonata* (Zetterstedt), and (34) *Paraprosalpia silvestris* (Fallén); (35) fore and (36) hind tarsi, dorsal views, of female of *Acrostilpna atricauda* (Zetterstedt); fore tarsus, dorsal views, of female of (37) *Paraprosalpia constrictor* (Malloch) and (38) *Eutrichota humeralis* (Stein); (39) ventral, (40) left lateral, and (41) dorsal views of female terminalia of *Anthomyia pluvialis* (Linnaeus); (42) terminal portion of ovipositor of *Leucophora johnsoni* (Stein), dorsal view; (43) terminal portion of ovipositor of *Phorbia sp.*, left lateral view.

Abbreviations: ad, anterodorsal; av, anteroventral; cerc, cercus; d, dorsal; epiprct, epiproct; hyprct, hypoproct; p, posterior; pd, posterodorsal; s, seta or bristle; spmth, spermatheca; spr, spiracle; st, sternite; tg, tergite.

25. Proboscis unusually long, slender, or tubular (Fig. 17) 26

Proboscis not very long, slender, or tubular (Figs. 15, 16) 27

26. Arista plumose, swollen at base .... ***Neohylemyia*** Malloch

1 sp., *proboscidalis* Malloch; Illinois

Arista nearly bare .... ***Proboscimyia*** Bigot

2 spp.; eastern, western; Huckett 1940

27. Eye more or less densely haired .... ***Alliopsis*** Schnabl & Dziedzicki

7 spp.; northern North America; Huckett 1965*a*

Eye bare or nearly so 28

28. Prementum usually large in both sexes (Fig. 16); head noticeably small. Scutellum seldom with ventral hairs .... ***Pycnoglossa*** Coquillett

9 spp.; eastern, one species also in Washington; Huckett 1949

Prementum not conspicuously enlarged in either sex; head of normal size. Scutellum always with ventral hairs 29

29. Longest aristal hairs, especially on dorsal side, longer than width of first flagellomere 30

Longest aristal hairs not longer than width of first flagellomere 32

30. Hind tibia with short apical posteroventral bristle. Proboscis rather stout .... ***Hylemyza*** Schnabl & Dziedzicki

1 sp., *partita* (Meigen); widespread

Hind tibia without apical posteroventral bristle. Proboscis normal 31

31. Katepisternal bristles arranged 1:2 (as in Fig. 19). Arista unusually swollen at base .... ***Ganperdea*** Aldrich

3 spp.; widespread; Steyskal 1967

Katepisternal bristles arranged 2:2 (as in Fig. 25). Arista not unusually swollen at base .... ***Hylemya*** Robineau-Desvoidy

2 spp.; widespread; Huckett 1965*a*, 1971

32. Hind tibia usually with two posterodorsal bristles (Fig. 33), exclusive of apical one, although one only in *Pegomya notabilis* (Zetterstedt) (Fig. 31); male without posteroventral setae on hind tibia. Female with wide frons 33

Hind tibia usually with one, three, or more than three posterodorsal bristles, exclusive of apical bristle; if with two such bristles in either sex, then male with one or more posteroventral setae on hind tibia and female with narrowed frons (Fig. 6) 38

33. Mid tibia with an anteroventral bristle, exclusive of apical bristles 34

Mid tibia without an anteroventral bristle, exclusive of apical bristles 35

34. Lower margin of face protruded beyond level of lower margin of frons (as in Fig. 12) .... ***Adia*** Robineau-Desvoidy, in part

as *Paregle* Schnabl; see couplet 13

Lower margin of face not protruded beyond level of lower margin of frons (as in Fig. 13) .... ***Pegomya*** Robineau-Desvoidy, in part

see couplet 22

35. C bounding cell c with numerous fine setulae on lower surface (as in Fig. 28). Cruciate interfrontal setae usually absent in one or both sexes .... ***Pegomya*** Robineau-Desvoidy, in part

Eutrichota Kowarz; see couplet 22

C bounding cell c mainly bare on lower surface (as in Fig. 27). Cruciate interfrontal setae (Fig. 2) usually present in both sexes 36

36. Prementum pruinose. Male with abdominal segment 5 of normal length; processes of sternite 5 dull and extensively bristled .... ***Nupedia*** Karl

10 spp.; widespread; Huckett 1965*a*

Prementum polished. Male with abdominal segment 5 shortened; processes of sternite 5 shiny and mostly without bristles 37

37. Fore tibia without bristles, except at apex. Apical setulae of scutellum distinctly stronger than ventral hairs (Fig. 23). Processes of male abdominal sternite 5 weakly developed and almost bare .... ***Pseudonupedia*** Ringdahl

1 sp., *intersecta* (Meigen); Michigan west to California

Fore tibia with one or more distinct bristles before apex. Apical setulae of scutellum weak and hair-like, similar in size to ventral hairs (Fig. 26). Processes of male abdominal sternite 5 strongly developed and bristled (Fig. 47) .... ***Paraprosalpia*** Villeneuve, in part

20 spp.; widespread; Huckett 1965*a*

38. Male (usually holoptic as in Fig. 4) 39

Female (usually dichoptic as in Fig. 2) 56

39. Hind tibia usually without posteroventral setae (but with single posterior bristle near middle in some *Paraprosalpia*, as in Fig. 34) 40

Hind tibia with one or more posteroventral setae 46

40. Cruciate interfrontal setae present, but sometimes difficult to distinguish from uppermost frontal setae. Eyes relatively broadly separated 41

Cruciate interfrontal setae absent (Fig. 4). Eyes practically contiguous 44

41. Processes of abdominal sternite 5 mostly bare, blade-like, and subparallel to one another, or in form of two upright prong-like claspers that are set widely apart at base (Fig. 47) .... ***Paraprosalpia*** Villeneuve, in part

see couplet 37

Processes of abdominal sternite 5 structurally otherwise (Figs. 44–46) 42

42. Legs with tibiae, at least, partly yellow .... ***Pegomya*** Robineau-Desvoidy, in part

see couplet 22

Legs with tibiae usually entirely blackish 43

43. Dorsal bristle of posterior anepisternal series long and strong (as in Fig. 20) .... ***Hydrophoria*** Robineau-Desvoidy, in part

see couplet 15

Dorsal bristle of posterior anepisternal series short and weak (as in Figs. 21, 22) 54

44. Notopleural depression with hairs or setulae in addition to usual bristles (as in Figs. 18, 19). Abdominal tergite 6 with several slender bristles .... ***Eremomyia*** Stein, in part

10 spp.; widespread; Huckett 1951, Griffiths 1984*b* (as *Eutrichota*)

Notopleural depression usually with two bristles only. Abdominal tergite 6 without bristles 45

45. Tibiae partly yellow. Terminalia, when viewed from behind, symmetric with remainder of abdomen .... ***Pegomya*** Robineau-Desvoidy, in part

see couplet 22

Tibiae blackish. Terminalia, when viewed from behind, asymmetric with remainder of abdomen .... ***Eremomyia*** Stein, in part

see couplet 44

46. Abdominal tergite 6 conspicuous, with numerous bristles; inner borders of processes of sternite 5 with submarginal series of spinules (Fig. 44) .... ***Botanophila*** Lioy, in part

20 spp.; widespread; Huckett 1947

Abdominal tergite 6 usually inconspicuous, typically without bristles (Fig. 49), except in *Pegohylemyia discreta* (Meigen); inner borders of processes of sternite 5 without submarginal series of spinules (Figs. 45, 46) 47

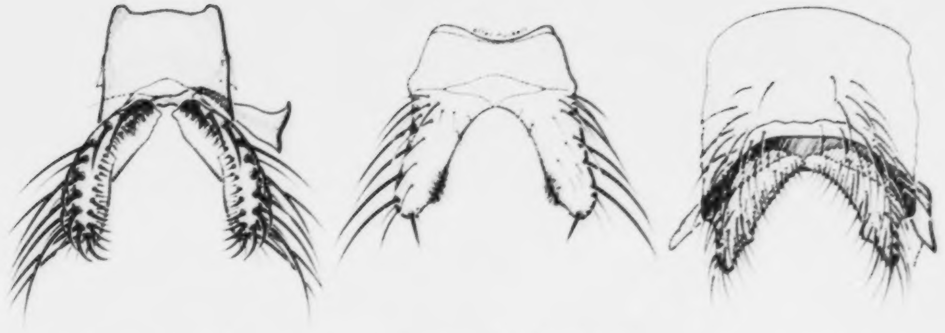
47. Hind tibia with apical posteroventral bristle (but very small in *Acrostilpna* Ringdahl) ... 48

Hind tibia without apical posteroventral bristle 50

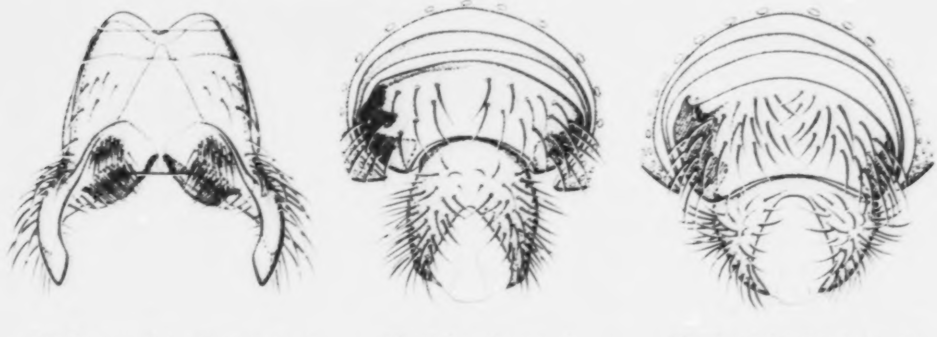
48. Processes of abdominal sternite 5 in form of thin pendant plates, and nearly devoid of bristles on outer border. Crossveins clouded except in *C. mimetica* (Malloch) .... ***Craspedochoeta*** Macquart, in part

5 spp.; widespread; Huckett 1946

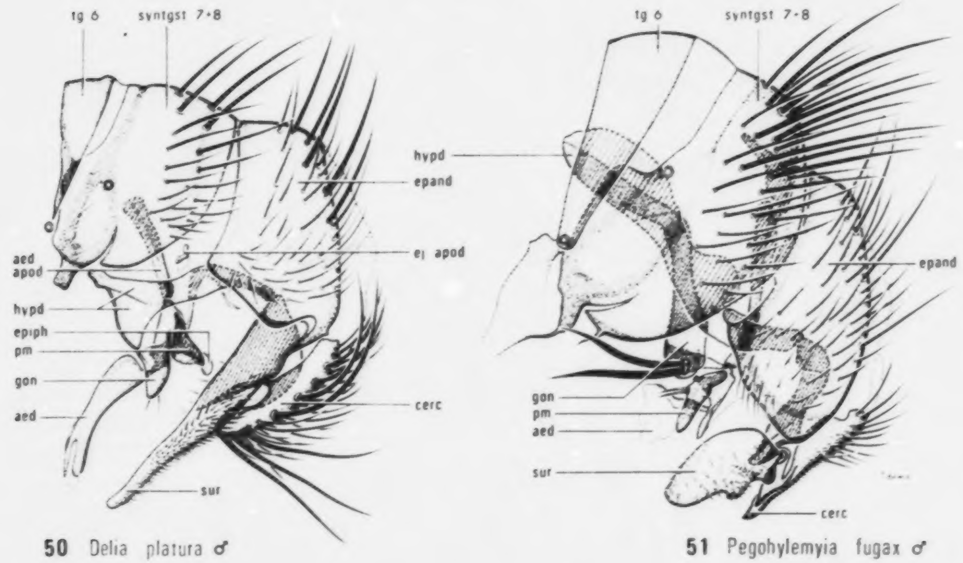
Processes of abdominal sternite 5 in form of posteriorly directed lobes, and with several bristles on outer border (Fig. 45). Crossveins never clouded 49



44 Botanophila spinidens ♂ **45** Phorbia nitidula ♂ **46** Egle muscaria ♂



47 Paraprosalpia constrictor ♂ **48** Delia platura ♂ **49** Pegohylemyia fugax ♂



tg 6
syntgst 7+8
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pm
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tg 6
syntgst 7-8
hypd
epand
gon
pm
aed
sur
cerc

50 Delia platura ♂ **51** Pegohylemyia fugax ♂

Figs. 104.44–51. Male terminalia: processes of sternite 5, ventral views, of (44) *Botanophila spinidens* (Malloch), (45) *Phorbia nitidula* (Coquillett), (46) *Egle muscaria* (Fabricius), and (47) *Paraprosalpia constrictor* (Malloch); epandrium and pregenital segments, posterodorsal views, of (48) *Delia platura* (Meigen) and (49) *Pegohylemyia fugax* (Meigen); lateral views of terminalia of (50) *Delia platura* and (51) *Pegohylemyia fugax*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; pm, paramere; sur, surstylus; syntgst, syntergosternite; tg, tergite.

49. Abdomen conical, not dorsoventrally depressed. Proboscis slender. Body grayish pruinose .... ***Acrostilpna*** Ringdahl, in part

7 spp.; widespread; Huckett 1946, 1965*a*

Abdomen dorsoventrally depressed. Proboscis usually not slender. Body blackish pruinose .... ***Lasiomma*** Stein, in part

7 spp.; widespread; Huckett 1965*a*, 1971

50. Processes of abdominal sternite 5 lengthy, notched or indented on inner border, and with fringe or mat of minute setulae on inner margin (Fig. 45). Eyes well-separated. Hairs on ventral surface of scutellum usually very sparse or absent. Proboscis subnormal in size (Fig. 15). Anterior postsutural supra-alar (prealar) bristle long (as in Figs. 18, 19). Terminalia enlarged and well-bristled dorsally .... ***Phorbia*** Robineau-Desvoidy, in part

11 spp.; widespread; Huckett 1948

Male without above combination of characters 51

51. Syntergosternite 7 + 8 polished and jet black.......................... go back to 49

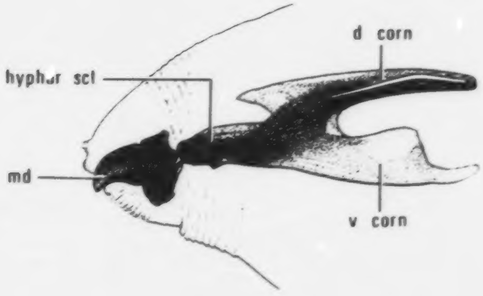
Syntergosternite 7 + 8 unpolished and dull gray, except in *Egle pilitibia* (Ringdahl) 52

52. Diminutive species, 3–4 mm long, with fine slender bristles. First flagellomere subquadrate. Lower margin of face protruded forward (Fig. 12). Fore tibia with one or more fine posterior bristles. Mid tibia without a ventral bristle near middle. Processes of abdominal sternite 5 set widely apart at base, weakly sclerotized (Fig. 46) .... ***Egle*** Robineau-Desvoidy, in part

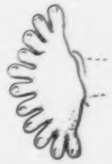
see couplet 17

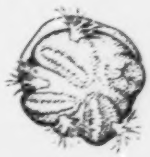
Male without above combination of characters 53

52 Delia radicum



53 Delia radicum





54 Delia radicum 55

Figs. 104.52–55. Larva of *Delia radicum* (Linnaeus): (52) mature larva, left lateral view; (53) details of cephalopharyngeal skeleton of mature larva, left lateral view; (54) left anterior spiracle, lateral view; (55) left posterior spiracle, dorsal view.

Abbreviations: d corn, dorsal cornu; hyphar scl, hypopharyngeal sclerite; md, mandible; v corn, ventral cornu.

53. Cheek and parafacial broad and buccate. Abdomen conical, scarcely longer than robust thorax. Postocular series of setulae discontinued along ventral margin of eye (Fig. 7). .... ***Leucophora*** Robineau-Desvoidy, in part

13 spp.; widespread; Huckett 1940

Cheek or parafacial, or both, usually less prominent; if both are broad, postocular series of setulae continued along ventral half of eye (as in Fig. 8) 54

54. Head at maximum length as long as or longer than high. Proboscis slender. Terminalia patterned after that of *Pegohylemyia* (see couplet 55) .... ***Macateeia*** Malloch, in part

1 sp., *atra* Malloch; California; see couplet 60 for second species

Head at maximum length shorter than high (Fig. 11) 55

55. Anepisternum usually with an outstanding setula below anterior notopleural bristle (as in Fig. 22). Mid tibia usually with two posterodorsal bristles. Dorsal region of occiput usually setose below postocular series of setulae (as in Fig. 5). Syntergosternite 7 + 8 of abdomen uniformly setose from margin to margin, more prominent than epandrium. Epandrium weakly setose throughout, oval in outline when viewed from behind (below in repose) (Fig. 49), strongly narrowed dorsally, and conforming with syntergosternite 7 + 8 when viewed from side (Fig. 51). .... ***Pegohylemyia*** Schnabl, in part

50 spp.; widespread; Huckett 1965*a*

Anepisternum usually without an outstanding setula below anterior notopleural bristle (Fig. 21). Mid tibia usually with one posterodorsal bristle, but if two present, dorsal region of occiput below postocular series of setulae bare or nearly bare. Syntergosternite 7 + 8 of abdomen with setae diverse and in transverse series on posterior half, becoming bare anteriorly. Epandrium with stronger setae dorsally, more or less conical in outline when viewed from behind (Fig. 48), little narrowed dorsally, and not conforming with syntergosternite 7 + 8 when viewed from side (Fig. 50) .... ***Delia*** Robineau-Desvoidy, in part

105 spp.; widespread; Huckett 1965*a*

56. Hind tibia with apical posteroventral bristle (very weak in *Acrostilpna* Ringdahl) 57

Hind tibia without apical posteroventral bristle 60

57. Tarsomere 5 of fore tarsus enlarged (Fig. 35), much larger than tarsomere 5 of mid tarsus (Fig. 36), except in *latipennis* (Zetterstedt). Prementum polished .... ***Acrostilpna*** Ringdahl, in part

see couplet 49

Tarsomere 5 of fore tarsus subequal to that of mid tarsus. Prementum usually pruinose 58

58. Presutural acrostichal bristles weak and setula-like; anterior postsutural supra-alar (prealar) bristle as long as anterior notopleural bristle (as in Figs. 18, 19) ... ***Botanophila*** Lioy, in part

see couplet 46

Presutural acrostichal bristles strong and bristle-like; anterior postsutural supra-alar bristle usually shorter than anterior notopleural bristle 59

59. Crossveins clouded, except in *C. mimetica* (Malloch); color of frontal vitta and fronto-orbital plates strongly contrasting .... ***Craspedochoeta*** Macquart, in part

see couplet 48

Crossveins unclouded; color of frontal vitta and fronto-orbital plates weakly contrasting ... . ***Lasiomma*** Stein, in part

see couplet 49

60. Head at maximum length as long as or longer than high. Proboscis slender .... ***Macateeia*** Malloch, in part

1 sp., *protuberans* Malloch; eastern; see couplet 54

Head at maximum length shorter than high. Proboscis not slender (Fig. 15) 61

61. Terminal segments of ovipositor sharply vertically flattened and weakly haired (Fig. 43) 62

Terminal segments of ovipositor not vertically flattened, variously haired (Figs. 39–42) 63

62. Abdomen black and shiny, unmarked .... ***Phorbia*** Robineau-Desvoidy, in part
see couplet 50

Abdomen grayish .... ***Pegohylemyia*** Schnabl, in part
see couplet 55

63. Terminal sclerites of ovipositor with recurrent spinules (Fig. 42) 64

Terminal sclerites of ovipositor without recurrent spinules (Figs. 39–41) 66

64. Dorsal bristle of posterior anepisternal series long and strong (Fig. 20). Prementum robust, polished .... ***Hydrophoria*** Robineau-Desvoidy, in part
see couplet 15

Dorsal bristle of posterior anepisternal series short and weak (Figs. 21, 22). Prementum variable 65

65. Cheek and parafacial broad and buccate; postocular series of setulae discontinued along ventral margin of eye (Fig. 7) .... ***Leucophora*** Robineau-Desvoidy, in part
see couplet 53

Cheek and parafacial usually not broad and buccate, but if these broad, postocular series of setulae continuous along ventral margin of eye (Fig. 8) .... ***Delia*** Robineau-Desvoidy, in part
see couplet 55

66. Tarsomere 5 of fore tarsus enlarged (Fig. 35), larger than tarsomere 5 of mid tarsus (Fig. 36) and wider than tarsomeres 3 and 4 of fore tarsus .... ***Acrostilpna*** Ringdahl, in part
see couplet 49

Tarsomere 5 of fore tarsus subequal to tarsomere 5 of mid tarsus, or if somewhat dilated, not wider than tarsomeres 3 and 4 of fore tarsus (Figs. 37, 38) 67

67. Apical setulae of scutellum weak and hair-like, similar in size to ventral hairs (Fig. 26). Prementum polished and slightly narrowed. Segment 5 of abdomen relatively short .... ***Paraprosalpia*** Villeneuve, in part
see couplet 37

Apical setulae of scutellum distinctly stronger than ventral hairs (Fig. 23). Other characters not as above 68

68. Cruciate interfrontal bristles absent 69

Cruciate interfrontal bristles present (as in Fig. 2) 71

69. Mid tibia with anteroventral bristle, and tarsomeres 3 and 4 of fore tarsus dilated and wider than tarsomere 5 (Fig. 38), except in *E. albidosa* Huckett .... ***Eremomyia*** Stein, in part
see couplet 44

Mid tibia without anteroventral bristle, or if so, tarsomeres 3 and 4 of fore tarsus not wider than tarsomere 5 70

70. Femora and tibiae mainly yellowish .... ***Pegomya*** Robineau-Desvoidy, in part
see couplet 22

Femora and tibiae blackish.............................. ***Eremomyia*** Stein, in part
see couplet 44

71. Tergite 5 with upright discal bristles; anepisternum with a weak but distinct bristle on upper border below anterior notopleural bristle (as in Fig. 20); katepisternal bristles usually arranged 2:2 (much as in Fig. 25); mid tibia with two posterodorsal bristles (as in Fig. 33). Proboscis not slender .... ***Pegohylemyia*** Schnabl, in part
see couplet 55

Not all of above characters present simultaneously 72

72. Mid tibia with two or more posterodorsal bristles; dorsal region of occiput with numerous setulae below postocular series (as in Fig. 5) 73

Mid tibia usually with one posterodorsal bristle; if two present, dorsal region of occiput sparsely setulose or mainly bare below postocular series, except in *Delia vesicata* (Huckett) 75

73. Cheek sharply tapered caudally below eye (Fig. 14); presutural and postsutural acrostichal bristles regularly paired throughout .... ***Lasiomma*** Stein, in part
see couplet 49

Cheek uniformly broad below eye (Fig. 11); acrostichal setulae not regularly paired throughout 74

74. C bounding cell c with numerous fine setulae on lower surface (Fig. 28) .... ***Botanophila*** Lioy, in part
see couplet 46

C bounding cell c mainly bare on lower surface (Fig. 27) .... ***Pegohylemyia*** Schnabl, in part
see couplet 55

75. Anepisternum usually without a short bristle on upper border below anterior notopleural bristle (Fig. 21), except in *D. hinei* (Malloch) .... ***Delia*** Robineau-Desvoidy, in part
see couplet 55

Anepisternum usually with a short bristle on upper border below anterior notopleural bristle (as in Fig. 20) 76

76. Tibiae mainly yellowish .... ***Pegomya*** Robineau-Desvoidy, in part
see couplet 22

Tibiae black .... ***Lasiomma*** Stein, in part
see couplet 49

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MUSCIDAE

105

H. C. Huckett and J. R. Vockeroth

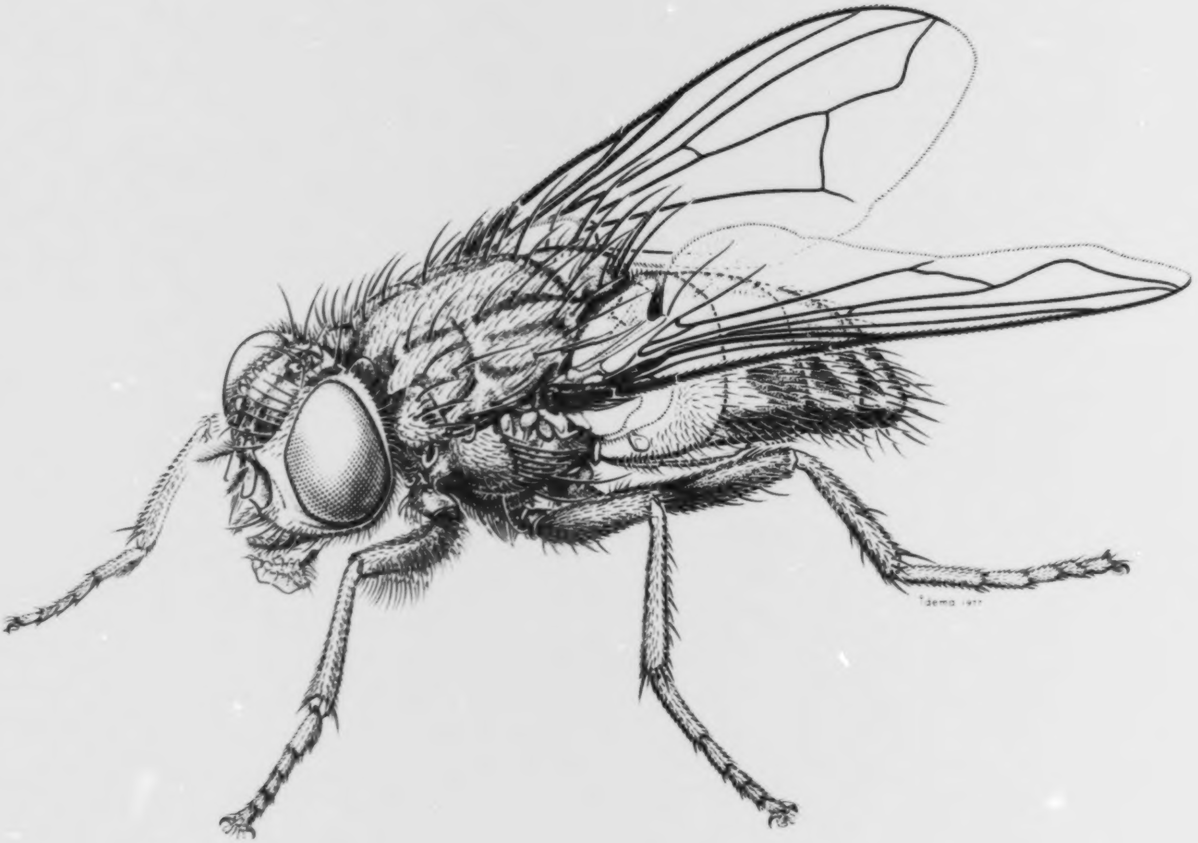

Fig. 105.1. Male of *Musca domestica* Linnaeus.

Slender to robust, usually strongly bristled flies (Fig. 1), usually dull in color, black, gray, or yellowish, sometimes bright metallic blue or green, rarely with brightly colored hairs and resembling bumble bees; wings usually unmarked, sometimes with crossveins clouded, rarely with more extensive markings. Length 2–14 mm.

Adult. Head: usually higher than long with frons sloping downward anteriorly (Figs. 2–5, 7–13), rarely subquadrate in profile with frons nearly horizontal (Fig. 6). Frons of male broad to very narrow; fronto-orbital plate always visible even if narrow, but frontal vitta sometimes partly obsolete. Frons of female at least one-fourth as wide as head; frontal vitta distinct, usually much wider than fronto-orbital plate. Broad-fronted males, and all females, with one to many medioclinate frontal bristles, with at most two proclinate to lateroclinate and two reclinate orbital bristles (if the two series overlap, the orbitals are lateral to the frontals), sometimes with one pair of cruciate interfrontal bristles, and usually with moderate to strong ocellar, inner vertical, outer vertical, and postocellar bristles. Narrow-fronted males with one to many medioclinate frontal bristles (the upper ones are sometimes slightly proclinate or reclinate), with orbital bristles very weak or absent, and with inner vertical, outer vertical, and postocellar bristles often weak and scarcely distinguishable from postocular setulae. Frons often with many fine setulae and hairs among the strong bristles, in a few exotic species with many short stiff setulae but without bristles. Parafacial usually bare, rarely with fine hairs or short setulae. Vibrissa usually strong, usually with many associated weaker bristles or hairs. Gena with few to many weak to strong subvibrissal setae below on entire length, and usually without outstanding genal bristles. Facial ridge usually with hairs only on lower part; face usually flat or concave, rarely with median keel or tubercle on upper part, usually bare but sometimes with a few short hairs below. Postcranium in Nearctic species with stiff black hairs on lower part. Eye bare or haired; male sometimes with facets of upper half enlarged. Antenna usually shorter than face and slender, but sometimes elongate or broadened; scape and pedicel short; pedicel with a distinct dorsal seam and sometimes flattened above (Fig. 14); first flagellomere at least twice as long as broad in Nearctic species, usually rounded apically but sometimes angulate apicodorsally; arista three-segmented, bare to long plumose or, rarely, pectinate. Proboscis well-developed, usually with fleshy labella, but in Stomoxyinae proboscis tapering to a slender apex and labella very small; palpus well-developed, sometimes thickened or broadened toward apex.

Thorax: bristles usually distinct and long, rarely with discal bristles very short or with most or all bristles hair-like and scarcely distinguishable from scutal hairs. Postpronotum with one or several bristles. Scutum with few to many short hairs and usually with the following bristles: one or two presutural and three or four postsutural dorsocentrals, two presutural intra-alars (often called the posthumeral bristle and presutural bristle), two postsutural intra-alars, two notopleurals, two or three postsutural supra-alars (the anterior one, when three are present, often called the prealar), and two postalars; acrostichal hairs in two to many rows, usually with a prescutellar pair and sometimes one or more other pairs bristle-like. Scutellum usually with two pairs of marginal bristles, rarely with one pair or with more than two pairs, sometimes with lateral hairs extending onto undersurface but never with an isolated group of hairs below apex. Laterotergite bare in Nearctic species; membrane between katatergite and base of lower calypter sometimes with a few strong hairs. Postalar wall and suprasquamal ridge rarely with short hairs (Fig. 17). Disc of propleuron usually bare, rarely with short hairs; proepisternum and proepimeron each with one or more bristles. Anepisternum sometimes with a weak anterodorsal bristle, always with a row of posterior bristles and with few to many hairs on posterodorsal half; katepisternum with one to four bristles variously arranged on upper posterior part, with several ventral bristles, and with variously distributed setae or hairs. Greater ampulla sometimes setulose. Anepimeron bare or with variously distributed hairs, rarely with a distinct bristle; katepimeron bare or haired; meron bare or with hairs in front of and below spiracle, with moderately distinct bristles only in some members of the Old World tribe Eginiini (subfamily Phaoniinae). Metepisternum bare or with a few fine hairs; metepimeron bare. Prosternum bare or haired, usually parallel-sided or nearly so (Fig. 19), rarely broadened anteriorly (Fig. 18) or, in some exotic species, strongly narrowed anteriorly; membrane between prosternum and propleuron usually bare, in some exotic species with one or several strong hairs; metasternal area bare or, rarely, with a few hairs. Posterior spiracle varied in size, shape, and nature of marginal vestiture.

Wing (Figs. 21–30) usually well-developed and with venation nearly constant, differing significantly only in course of Sc, M, and A_2. Vein A_1 always incomplete; wing markedly reduced only in one subantarctic species of *Coenosia* Meigen. C with costagial, humeral, and subcostal breaks, usually ending at apex of M but rarely ending before this point. Some veins, especially on anterobasal part of wing, with setae above or below, or both; wing membrane usually entirely covered with microtrichia, sometimes with bare areas near base. Lower calypter usually with posterior margin rounded or subtruncate (Figs. 15, 16) and usually extending beyond margin of upper calypter; posterior margin quite straight only in some species of Fanniinae; upper surface of lower calypter with fine hairs in some exotic species.

Legs (Figs. 31–43) usually slender; those of male sometimes with marked modifications of various segments or, rarely, of tarsal claws; tarsomeres of foreleg of female sometimes broadened. Legs with varied and taxonomically important vestiture of bristles and setulae (a strong posterodorsal bristle at about two-thirds length of hind tibia (Fig. 34) is often called the calcar); tarsomere 1 of hindleg without the prominent subbasal ventral bristle that is present in most Anthomyiidae.

Abdomen: tergites 1–5 exposed in both sexes, usually with strong marginal bristles and sometimes with discal bristles. Sternites 1–5 usually exposed; sternite 1 bare or haired.

Male (Fig. 47) with sternite 4 rarely modified; sternite 5 posteriorly shallowly emarginate to deeply bilobate, usually nearly flat and little ornamented but sometimes very elaborate. Sclerites of segments 6–8 usually asymmetric but symmetric and with varied sclerotization in Fanniinae, in some Coenosiinae, and in some species of *Lispe* Latreille; when these asymmetric, sternite 6 lying mostly to the left of the midventral line and often with its left end broad, sternite 7 small and left lateral in position between sternites 6 and syntergosternite 8 and firmly fused to both, and syntergosternite 8 dorsal and symmetric or nearly so; sternites 6 and 7 bare; syntergosternite 8 usually with many bristles and setulae, but bare in *Lispe* (if present); tergite 6 usually distinctly dorsal in position, symmetric, more or less fused with syntergosternite 8, usually bare but with bristles and hairs in some Coenosiinae, and rarely absent or indistinguishable; tergites 7 and 8 absent or indistinguishably fused with their sternites. Spiracles 1–5 situated in margins of tergites 1–5; spiracle 6 usually in or near lateral margin of tergite 6, left spiracle 7 usually in sternite 7, and right spiracle 7 usually in or near lateral margin of syntergosternite 8; in some species of *Lispe* spiracles 6 and 7 situated in margin of epandrium (tergite 9). Epandrium well-developed, its posterior surface directed ventrally in repose. Surstylus usually distinct, articulated with lower margin of epandrium, varied in shape, in some species of *Lispe* apparently fused with epandrium or lost by reduction. Hypandrium varied in shape, usually a rather flat or deep plate, but in some Coenosiinae in the form of a long bent cylinder linked posterolaterally to base of surstylus directly or through a bacilliform sclerite; aedeagus ranging from a membranous sac to a complex sclerotized structure sometimes bearing strong spines; epiphallus present or absent; aedeagal apodeme well-developed; ejaculatory apodeme usually present but absent in Fanniinae; gonopod usually distinct, articulated, or partly fused with hypandrium and projecting beyond its surface, with strong or minute setae, sometimes indistinguishably fused with hypandrium; paramere distinct, articulated, sometimes very elongate and spine-like, usually with distinct setae. Cerci separate or partly or entirely fused into a median plate, well-sclerotized, sometimes very elongate.

Female (Figs. 48, 49) terminalia variable in length, usually elongate and telescoped into segment 5 in repose, but sometimes very short and mostly exposed. Spiracles 1–5 situated in margins of tergites 1–5; spiracles 6 and 7 present in Fanniinae, usually both in tergite 6 but sometimes in membrane in front of or behind it; spiracle 6 present in a few exotic species of several subfamilies; spiracles 6 and 7 otherwise absent; some species of Eginiini sometimes with functional spiracles reduced in number or absent. Tergites and sternites of segments 6–8 often in the form of long slender struts but variable in shape and extent of sclerotization and sometimes unsclerotized, sometimes with strong apical spines; tergites 6–8 entire or divided medially; sternites 6 and 7 entire, but sometimes with a pair of detached apical portions; sternite 8 almost always divided medially, entire only in Eginiini and in some Fanniinae; in some species of *Cyrtoneurina* Macquart (Neotropical) each half of sternite 8 very strongly sclerotized and with apical teeth; sclerites of segments 7 and 8 fused in some Coenosiinae; intersegmental membranes long or short, that between segments 7 and 8 sometimes expanded below and with dense retrorse spicules. Cerci well-developed, either subcylindrical with inner surface sclerotized and haired on apical half or compressed with inner surface membranous and without hairs. Epiproct usually a flat triangular plate, rarely entirely membranous; hypoproct usually nearly flat, subtriangular or subpentagonal, sometimes with anterior or posterior portions curved upward, sometimes with two or more spinose setae at apex. Usually three sclerotized spermathecae present, two only present in some Fanniinae, usually subspherical to subcylindrical, sometimes with apex flattened or indented.

Egg. Pale, usually elongate oval, nearly flat below and rounded above (usually deposited with the ventral surface uppermost), below with a pair of weak ridges or narrow to broad submedian to lateral flanges on at least the anterior third of the egg and often on most or all of its length; these ridges or flanges sometimes meeting anteriorly and projecting as a median process or projecting as a pair of tapering sublateral processes that may be longer than the body of the egg and may have a median process between them. Eggs of the Eginiini short oval, convex above and concave below, with a large ventral pore. Surface of egg, flanges, and anterior filaments with varied surface sculpturing of taxonomic importance. Many eggs illustrated by van Emden (1965) and by Vockeroth (1972).

Larva. Subcylindrical (Fig. 51) or somewhat depressed (Fig. 50), tapering anteriorly, with cuticular thickening, ridges, and spicules. Mandibles (Fig. 54) usually fused or appressed, separated in Fanniinae, equal or unequal in size; accessory mandibular sclerites often present but absent in Fanniinae, Stomoxyinae, and some Muscinae; dental sclerite at base of mandible separate or fused; hypopharyngeal sclerite well-developed; parastomal bars absent; dorsal and ventral cornua of tentoropharyngeal sclerite subequal in length, both without lacunal aperture. Abdominal segments with ventral creeping welts; segment 8 sometimes with a pair of prolegs; apical segment with peripheral ring of papillae absent, indistinct or incomplete, rounded, subtruncate, or produced into a pair of spiracular processes; in Fanniinae (Fig. 50) body segments flattened or broadened, with branched or plumose lateral and apical, and often dorsal, appendages. Anterior spiracles palmate. Posterior spiracle with three openings arranged in an arc around the ecdysial scar; these openings more or less sinuate or serpentine in Stomoxyinae, most Muscini (Fig. 51), and some Cyrtoneurininae, usually slightly bent or elongate oval in other species (Fig. 52).

Biology and behavior. Larvae occur in many habitats: dung; decaying vegetation of many kinds, from fruit to logs; fungi; nests of birds, animals, and Hymenoptera; dry to wet soil; fresh water; dead snails or other carrion; and rarely, in the tissues of living plants. Actual larval food is known for rather few species; most are apparently coprophagous or saprophagous or are either facultative or obligatory predators of insect larvae or other invertebrates. A few species feed on nestling birds and a few on tissues of Gramineae. At least one species of the Old World tribe Eginiini is an endoparasite of millipedes. Larvae of a few species cause enteric or other myiases in humans or other vertebrates (James 1948). Eggs, or in a few species larvae in the first or later instar, are deposited on, or inserted in, the substrate, which provides larval food. Eggs usually produce a first-instar larva but sometimes a second- or third-instar larva.

Adults are predacious on other insects, pollenophagous, bloodsucking, or saprophagous on dung or decaying plant or animal matter, or they feed on exudations from vertebrates, especially large mammals. Species that take vertebrate blood or exudates are often severe nuisances or important vectors of parasites. Enteric or other diseases are often transmitted by species that feed on human feces or other waste matter. An extensive account of the medical importance of the family is given by Greenberg (1971, 1973), a brief summary by Pont (1973), and an account of the biology of *Musca* by West (1951).

Males of many species of Fanniinae and of a few other genera form aerial swarms that are presumably involved in mating. Mating behavior has, however, been observed in very few species of the family.

Classification and distribution. The suprageneric classification of the Muscidae developed during the early part of this century by Stein and Malloch and others was adapted by most workers, such as Huckett (1965, 1975) for the Nearctic fauna and by Hennig (1955–1964) for the Palaearctic fauna. Hennig (1965) revised the classification extensively, making particular use of head bristling and ovipositor structure. This classification, with slight modifications, has been adopted by most workers. The relationships of the Cyrtoneurininae, with 15 genera in the Neotropical region and the southern part of the Nearctic region, are uncertain; it seems likely that at least some of the genera should be referred to other subfamilies. The small Old World tribe Eginiini was not considered by Hennig; its position is doubtful, but it should probably be referred to the Muscidae. The very distinctive subfamily Fanniinae has recently been treated as a separate family by some workers; if, as Hennig suggests, it is a sister group of other Muscidae such treatment is reasonable but not essential. The classification of the Nearctic fauna at the generic level seems to be reasonably stable. The subgenera of *Coenosia* are probably artificial segregates; they are adopted here to facilitate the use of existing keys to species. Some large, nearly worldwide genera such as *Coenosia*, *Limnophora* Robineau-Desvoidy, *Helina* Robineau-Desvoidy, and *Phaonia* Robineau-Desvoidy are perhaps aggregates of distinct genera; a study of the world fauna will be necessary to clarify the matter. *Helina* and *Phaonia* are sometimes difficult to distinguish; the two genera should perhaps be redefined or even joined. The most important paper on the taxonomy of Nearctic Muscidae is that of Huckett (1965); it treats most Canadian genera and species and is not referred to under the individual genera in the key below. Huckett (1975) is useful for identification of western specimens.

Muscidae are nearly world wide in distribution. They are abundant on all continents, occur on most oceanic islands, and have many species on arctic and alpine tundra. Many species, especially those whose larvae live in dung or feces, have been widely distributed by man. In the Nearctic region there are 49 genera and 708 species; of these, six genera and at least ten species have almost certainly been accidentally introduced from the Old World. Only one genus, *Pentacricia* Stein, is restricted to the Nearctic region. Approximately 170 species (24% of the Nearctic fauna) are apparently naturally Holarctic in distribution. Hennig (1966) reviewed the fossils referred to the Muscidae and concluded that only one specimen, from Baltic amber, is definitely referable to the family. This specimen cannot be distinguished from those of the extant species *Fannia scalaris* (Fabricius).

Key to genera[1]

1. Anepimeron with few to many fine hairs 2
Anepimeron bare 15

2. Proboscis elongate, strongly sclerotized, tapering from a broad base to a slender apex and with labella atrophied (Fig. 2). Arista with long hairs above and bare or with a single hair below (Fig. 2) 3
Proboscis moderately or weakly sclerotized, not tapering strongly to apex, and with labella well-developed and often fleshy (Figs. 3–13). Arista uniformly haired above and below (Figs. 3–13) 5

3. Palpus about three-quarters as long as labium (Fig. 2). Meron and disc of propleuron bare 4
Palpus about one-third as long as labium. Meron and disc of propleuron haired .... ***Stomoxys*** Geoffroy
1 sp., *calcitrans* (Linnaeus); widespread

4. Notopleuron with hairs in addition to the two bristles. R_1 setulose above .... ***Haematobosca*** Bezzi
1 sp., *alcis* (Snow); widespread
Notopleuron without hairs, with only two bristles. R_1 bare above .... ***Haematobia*** Lepeletier & Serville
1 sp., *irritans* (Linnaeus); widespread

5. Lower calypter narrow, rounded posteriorly, with its anteromedian angle distinctly lateral to base of scutellum (Fig. 15) 6
Lower calypter broad, subtruncate posteriorly, with its anteromedian angle extending at least slightly under base of scutellum (Fig. 16) 10

6. Parafacial with one or more irregular rows of fine hairs throughout most or all of its length. Palpus moderately to strongly broadened apically (Fig. 3). Frons of male about one-third as wide as head .... ***Lispe*** Latreille
25 spp.; widespread; Snyder 1954

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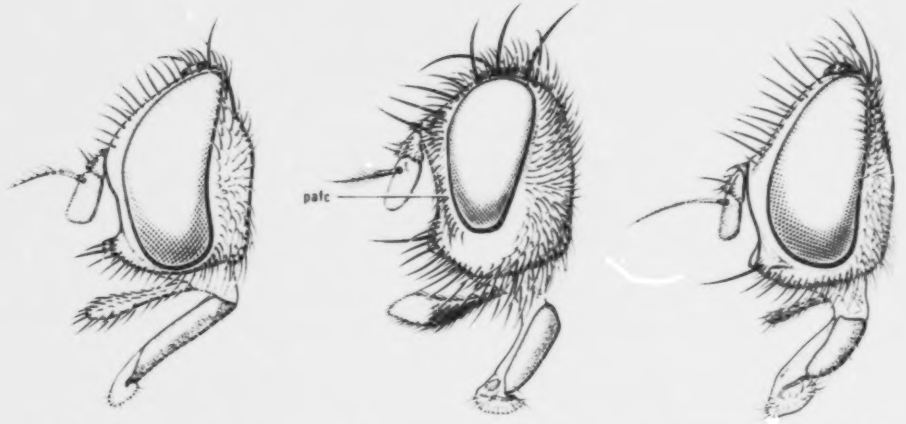
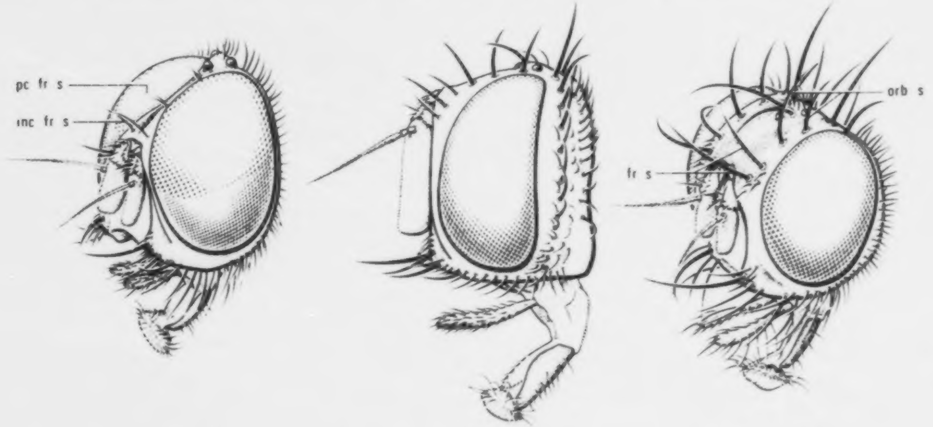
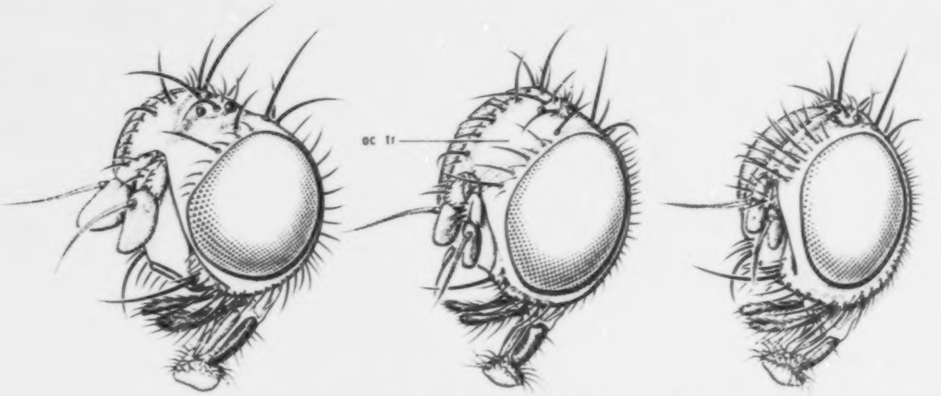
[1] The following changes in generic names proposed by Pont (1984) are adopted here: *Brontaea* Kowarz for *Gymnodia* Robineau-Desvoidy, *Caricea* Robineau-Desvoidy for *Lispocephala* Pokorny, *Neomyia* Walker for *Orthellia* Robineau-Desvoidy, and *Potamia* Robineau-Desvoidy for *Dendrophaonia* Malloch.
Recently proposed generic synonyms (Pont 1984, Vockeroth 1984) are the following: *Drymeia* Meigen (syn. *Bebryx* Gistel, *Eupogonomyia* Malloch, *Pogonomyia* Rondani, *Pogonomyioides* Malloch, *Trichopticoides* Ringdahl), *Fannia* Robineau-Desvoidy (syn. *Coelomyia* Haliday), *Helina* Robineau-Desvoidy (syn. *Quadrularia* Huckett), *Hydrotaea* Robineau-Desvoidy (syn. *Neohydrotaea* Malloch, *Ophyra* Robineau-Desvoidy), *Limnophora* Robineau-Desvoidy (syn. *Bucephalomyia* Malloch, *Pseudolimnophora* Strobl), *Piezura* Rondani (syn. *Platycoenosia* Strobl), Phaonia Robineau-Desvoidy (syn. *Bigotomyia* Malloch, *Plexiopsis* Huckett), and *Spilogona* Schnabl (syn. *Mydaeina* Malloch).



2 Haematobosca alcis ♂ **3** Lispe canadensis ♂ **4** Fannia subpellucens ♂



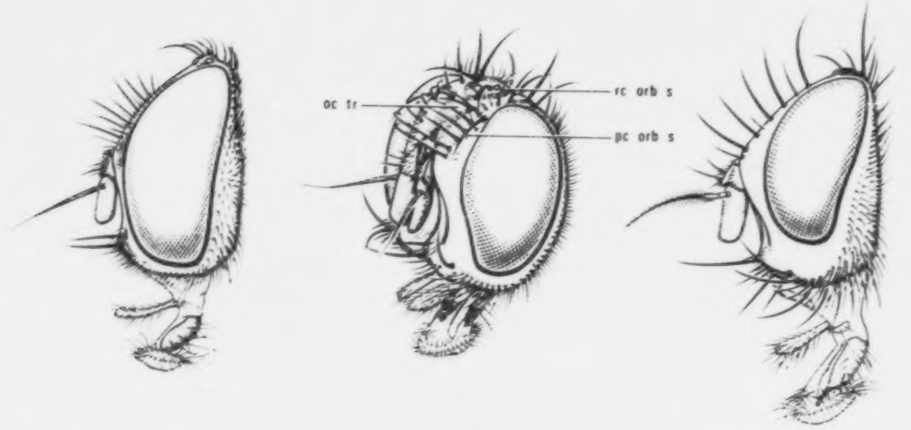
5 Azelia cilipes ♂ **6** Atherigona orientalis ♂ **7** Caricea alma ♂



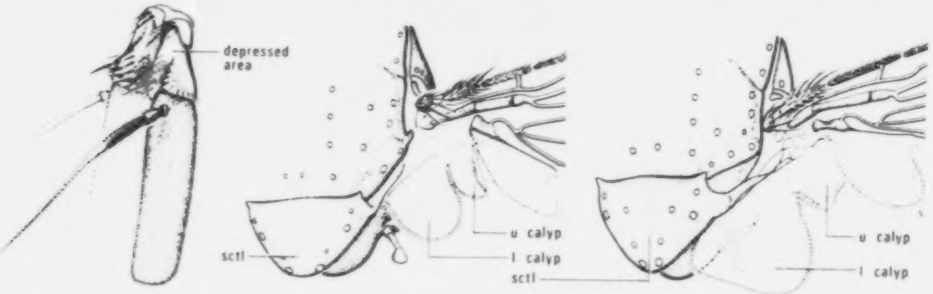
8 Schoenomyza dorsalis ♂ **9** Limnospila albifrons ♂ **10** Pseudocoenosia fletcheri ♂

Figs. 105.2–10. Heads: lateral views of (2) *Haematobosca alcis* (Snow), (3) *Lispe canadensis* Snyder, and (4) *Fannia subpellucens* (Zetterstedt); (5) anterodorsal view of *Azelia cilipes* (Haliday); (6) lateral view of *Atherigona orientalis* Schiner; anterodorsal views of (7) *Caricea alma* (Meigen), (8) *Schoenomyza dorsalis* Loew, (9) *Limnospila albifrons* (Zetterstedt), and (10) *Pseudocoenosia fletcheri* (Malloch) (*continued*).

Abbreviations: fr s, frontal bristle; inc fr s, inclinate frontal bristle; oc tr, ocellar triangle; orb s, orbital bristle; pafc, parafacial; pc fr s, proclinate frontal bristle.


oc tr
rc orb s
pc orb s

11 Hydrotaea ignava ♂ 12 Hydrotaea anxia ♀ 13 Potamia scabra ♂


depressed area
sctl
u calyp
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sctl
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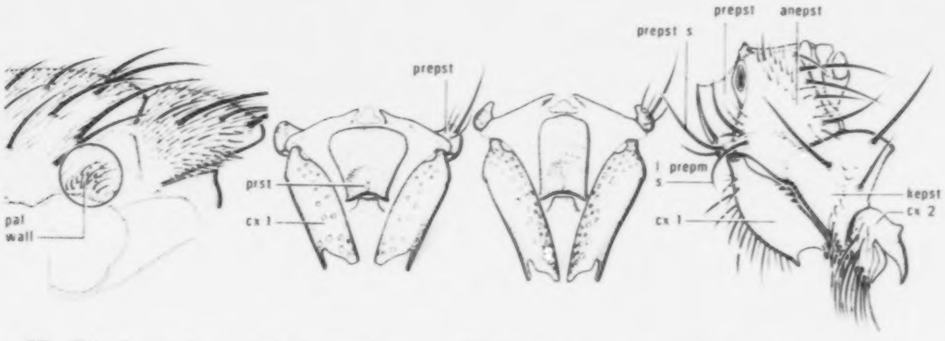
l calyp

14 Tetramerinx littoralis ♂ 15 Neomuscina tripunctata ♂ 16 Musca domestica ♂


pal wall
prepst
prst
cx 1
prepst s
prepst
anepst
l prepm s
cx 1
kepst
cx 2

17 Philornis sp. ♀ 18 Lophosceles cinereiventris ♀ 19 Phaonia bysia ♀ 20 Coenosia (Coenosia) tigrina ♂

Figs. 105.11–20. Heads (*concluded*) and thoracic structures: heads of (11) *Hydrotaea ignava* (Harris) in lateral view, (12) *Hydrotaea anxia* (Zetterstedt) in anterodorsal view, and (13) *Potamia scabra* (Giglio-Tos) in lateral view; (14) antenna of *Tetramerinx littoralis* (Malloch); calypteres and associated structures of (15) *Neomuscina tripunctata* (Wulp) and (16) *Musca domestica* Linnaeus; (17) postalar wall and associated structures of *Philornis* sp.; prosternum and associated structures of (18) *Lophosceles cinereiventris* (Zetterstedt) and (19) *Phaonia bysia* (Walker); (20) anterior part of pleura of *Coenosia* (*Coenosia*) *tigrina* (Fabricius) in lateral view.

Abbreviations: anepst, anepisternum; cx, coxa; kepst, katepisternum; l calyp, lower calypter; l prepm s, lower proepimeral bristle; oc tr, ocellar triangle; pal wall, postalar wall; pc orb s, proclinate orbital bristle; prepst, proepisternum; prepst s, proepisternal bristle; prst, prosternum; rc orb s, reclinate orbital bristle; sctl, scutellum; u calyp, upper calypter.

Parafacial bare. Palpus slender or very slightly broadened apically. Frons of male at most one-sixth as wide as head 7

7. Hind tibia with three or more posterodorsal bristles that are at least as long as anterodorsal bristles and are more or less uniformly spaced along length of tibia (Fig. 32) . . . . ***Drymeia*** Meigen, in part
20 spp.; widespread; Malloch 1918 (as *Pogonomyia* Rondani)

Hind tibia with at most one posterodorsal bristle at about two-thirds length of tibia 8

8. Apical section of M curved strongly forward, making cell r_{4+5} narrower at wing margin than at a point opposite crossvein dm-cu (Fig. 21). Hind tibia without posterodorsal bristle . . . . ***Neomuscina*** Townsend
2 spp.; Florida, Texas

Apical section of M curved at most very slightly forward, making cell r_{4+5} wider at wing margin than at a point opposite crossvein dm-cu. Hind tibia with strong posterodorsal bristle at about two-thirds its length (as in Fig. 34) 9

9. Prosternum and meron haired. R_1 and R_{4+5} setulose above . . . . ***Polietina*** Schnabl & Dziedzicki
1 sp., *pruinosa* (Macquart); southern Texas

Prosternum and meron bare. R_1 and R_{4+5} bare above . . . . ***Polietes*** Rondani
2 spp.; widespread; Malloch 1923 (as *Pseudophaonia* Malloch)

10. Apical section of M bent sharply forward (Fig. 22). Prosternum haired 11

Apical section of M curved broadly forward (Fig. 23). Prosternum bare 12

11. Mid tibia with strong ventral bristle at about two-thirds its length. Scutum with a pair of strong presutural acrostichal bristles. Body metallic green . . . . ***Neomyia*** Walker
1 sp., *cornicina* (Fabricius); widespread

Mid tibia without ventral bristle. Scutum without presutural acrostichal bristles. Body not metallic, predominantly gray . . . . ***Musca*** Linnaeus
2 spp.; widespread; Vockeroth 1953, Sabrosky 1959

12. Calypteres and base of wing densely yellow. Vestiture of scutum, scutellum, and abdomen consisting of very dense and fine hairs . . . . ***Mesembrina*** Meigen
2 spp.; widespread

Calypteres and base of wing not densely yellow. Vestiture normal, consisting of strong bristles and weaker hairs 13

13. Mid tibia with strong posteroventral bristle at two-thirds its length. Body metallic blue or blue green . . . . ***Eudasyphora*** Townsend
3 spp.; widespread; Cuny 1980

Mid tibia without posteroventral bristle. Body usually not metallic 14

14. M ending slightly before apex of wing (Fig. 23). Postalar wall bare . . . . ***Morellia*** Robineau-Desvoidy
3 spp.; widespread

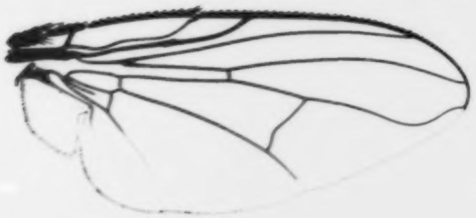
M ending far behind apex of wing (Fig. 24). Postalar wall haired (Fig. 17) . . . . ***Philornis*** Meinert
2 spp.; Florida, Texas

15. Hind tibia with middorsal bristle near midlength as well as with preapical middorsal bristle (Fig. 31). Sc diverging from R_1 at a point very near base of both veins; A_1, if extended, meeting extension of A_2 before wing margin (Figs. 25, 26) 16

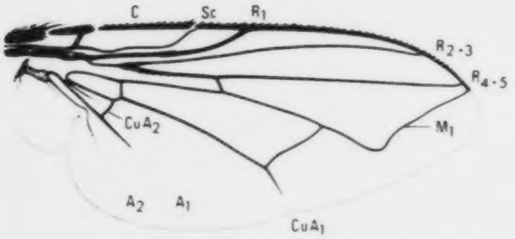
Hind tibia with preapical middorsal bristle only; this bristle usually very near apex but sometimes at about two-thirds length of tibia (Figs. 32–34). Sc very close to R over most of its length, diverging from it only near apex of Sc; A_1, if extended, not meeting extension of A_2 (Figs. 27–30) 18

16. Arista plumose. Katepisternum usually with a third weaker bristle present between and slightly below the two strong upper bristles . . . . ***Piezura*** Rondani
3 spp.; widespread; Chillcott 1961 (including *Platycoenosia* Strobl)

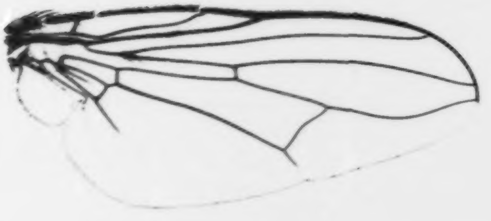
Arista pubescent or bare (Fig. 4). Katepisternum with only two bristles 17



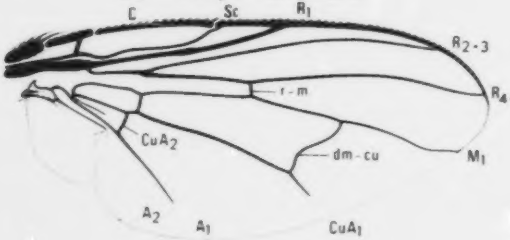
21 Neomuscina tripunctata ♂


C
Sc
R1
R2-3
R4-5
M1
CuA2
A2
A1
CuA1

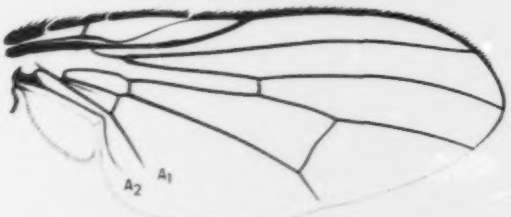
22 Neomyia cornicina ♂



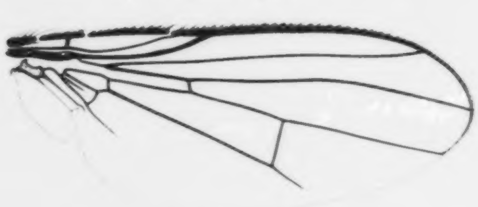
23 Morellia podagrica ♂


C
Sc
R1
R2-3
r-m
R4-5
CuA2
dm-cu
M1
A2
A1
CuA1

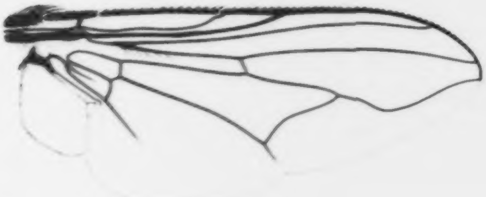
24 Philornis sp. ♀



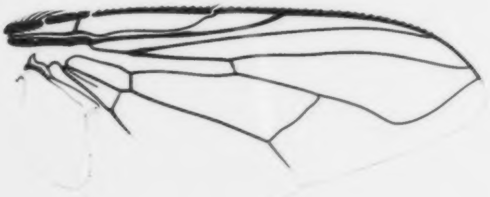
25 Fannia canicularis ♂



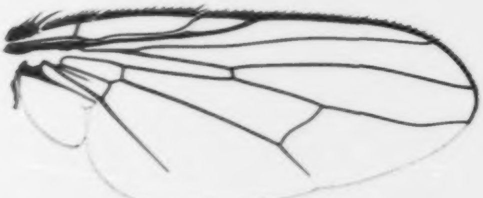
26 Euryomma peregrinum ♀



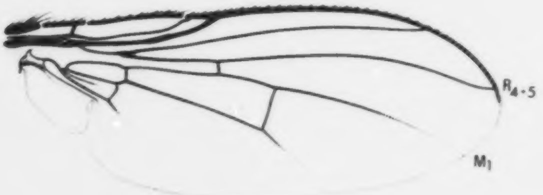
27 Graphomya idessa ♂



28 Synthesiomyia nudiseta ♂

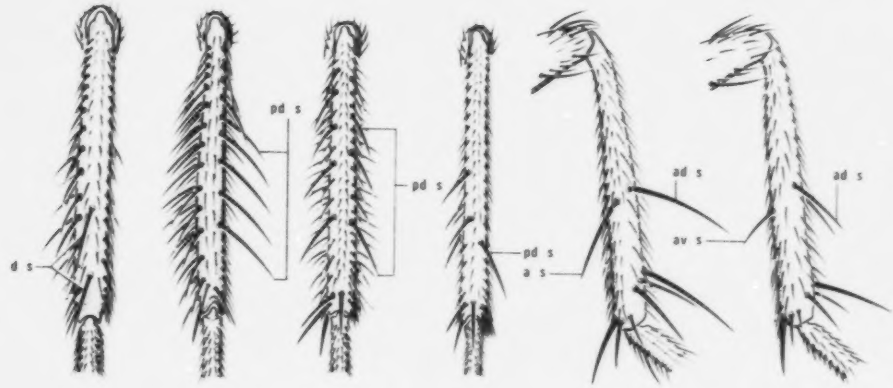


29 Muscina levida ♂

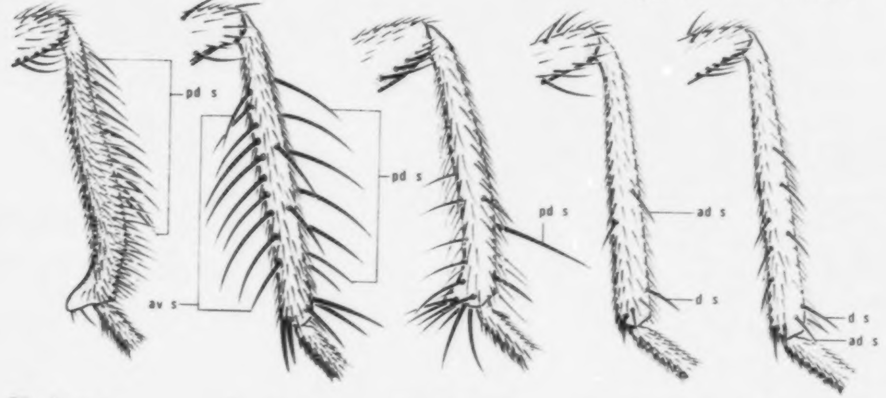


30 Allognota semivitta ♂

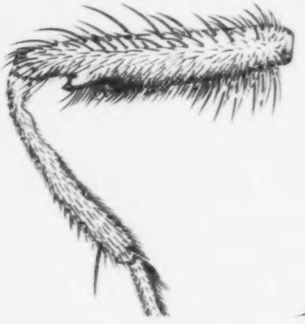
Figs. 105.21-30. Wings: (21) *Neomuscina tripunctata* (Wulp); (22) *Neomyia cornicina* (Fabricius); (23) *Morellia podagrica* (Loew); (24) *Philornis* sp.; (25) *Fannia canicularis* (Linnaeus); (26) *Euryomma peregrinum* (Meigen); (27) *Graphomya idessa* (Walker); (28) *Synthesiomyia nudiseta* (Wulp); (29) *Muscina levida* (Harris); (30) *Allognota semivitta* Malloch.



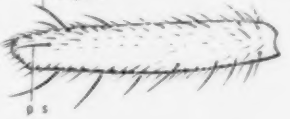
31 Fannia scalaris ♂ 32 Drymeia quadrisetosa ♂ 33 Phaonia deleta ♂ 34 Phaonia bysia ♂ 35 Coenosia (Coenosia) tigrina ♂ 36 Coenosia (Limosia) triseta ♂



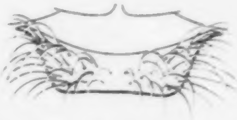
37 Drymeia groenlandica ♂ 38 Helina squalens ♂ 39 Hydrotaea ponti ♂ 40 Brontaea humilis ♂ 41 Spilogona almquisti ♂



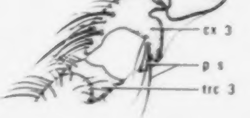
42 Hydrotaea anxia ♂



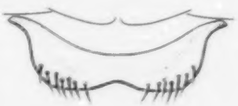
43 Coenosia (Neodexiopsis) ovata ♂



44 Lispoides aequifrons ♂



45 Thricops innocuus ♂



46 Brontaea humilis ♂

Figs. 105.31–46. Leg segments and sternites: hind tibiae in dorsal view of (31) *Fannia scalaris* (Fabricius), (32) *Drymeia quadrisetosa* (Malloch), (33) *Phaonia deleta* (Stein), and (34) *Phaonia bysia* (Walker); hind tibiae in anterior view of (35) *Coenosia (Coenosia) tigrina* (Fabricius), (36) *Coenosia (Limosia) triseta* Stein, (37) *Drymeia groenlandica* (Lundbeck), (38) *Helina squalens* (Zetterstedt), (39) *Hydrotaea ponti* Vockeroth, (40) *Brontaea humilis* (Zetterstedt), and (41) *Spilogona almquisti* Holmgren; (42) fore femur and tibia of *Hydrotaea anxia* (Zetterstedt) in posterior view; (43) hind femur of *Coenosia (Neodexiopsis) ovata* Stein in posterior view; (45) hind coxa of *Thricops innocuus* (Zetterstedt) in posterolateral view; sternite 1 in ventral view of (44) *Lispoides aequifrons* (Stein) and (46) *Brontaea humilis*.

Abbreviations: ad s, anterodorsal bristle; a s, anterior bristle; av s, anteroventral bristle; cx, coxa; d s, dorsal bristle; pd s, posterodorsal bristle; p s, posterior bristle; trc, trochanter.

17. Imaginary extensions of A_1 and A_2 meeting well before margin of wing (Fig. 25). First presutural dorsocentral bristle usually over half as long as second. Lower orbital bristle absent in male. Lower margin of face sometimes protruding (Fig. 4) .... **Fannia** Robineau-Desvoidy

100 spp.; widespread; Chillcott 1961 (including *Coelomyia* Haliday)

Imaginary extensions of A_1 and A_2 meeting at or near margin of wing (Fig. 26). First presutural dorsocentral bristle weak, less than half as long as second. Lower orbital bristle present in male. Lower margin of face not protruding .... **Euryomma** Stein

2 spp.; widespread; Chillcott 1961

18. Hind coxa with a row of setae near lower margin of posterior surface (Fig. 45) 19

Hind coxa without setae on posterior surface 20

19. One inclinate frontal bristle present (Fig. 5). A_1 short, ending rather abruptly not more than halfway between apex of cell cu*p* and wing margin. Hind tibia without posterodorsal bristle .... **Azelia** Robineau-Desvoidy

5 spp.; widespread

More than one inclinate frontal bristle present. A_1 extending more than halfway to wing margin. Hind tibia with one or more posterodorsal bristles (as in Figs. 33, 34) .... **Thricops** Rondani

14 spp.; widespread; Malloch 1921*a* (as *Trichopticus* Rondani)

20. Node of Rs, and often base of R_{4+5}, with one or more setulae above (Fig. 27) 21

Node of Rs and base of R_{4+5} bare above (Fig. 28) 27

21. Prosternum haired laterally. First postsutural supra-alar bristle absent .... **Limnophora** Robineau-Desvoidy

10 spp.; widespread; Huckett 1932

Prosternum bare. First postsutural supra-alar bristle present or absent 22

22. Last section of M curved distinctly forward (Fig. 27) 23

Last section of M not at all curved forward 25

23. Katepisternum with two posterior bristles only, the anterior one absent; katepimeron and meron with coarse black hairs. Eye haired at least above ..... **Graphomya** Robineau-Desvoidy

9 spp.; widespread; Arntfield 1975

Katepisternum with three or four bristles; katepimeron and meron bare. Eye haired or bare 24

24. Hind tibia with strong posterodorsal bristle at about three-fourths its length (Fig. 37) .... **Phaonia** Robineau-Desvoidy, in part

81 spp.; widespread; Malloch 1923

Hind tibia without posterodorsal bristle .... **Myospila** Rondani

1 sp., *meditabunda* (Fabricius); widespread

25. Katepisternum with two bristles, both near upper margin. Legs black. Female with ocellar triangle shining black and extending to anterior margin of frons ..... **Spilogona** Schnabl, in part

135 spp., but only 1 sp., *obscura* (Malloch), keys out here; widespread; Huckett 1932

Katepisternum with three or four bristles. Legs black or partly or entirely yellow. Female with ocellar triangle pruinose, extending at most a little in front of anterior ocellus 26

26. Eye bare or with minute hairs that are separated from one another by more than their length .... **Mydaea** Robineau-Desvoidy

31 spp.; widespread; Snyder 1949*b*

Eye with abundant and distinct hairs that are separated from one another by less than their length .... **Opsolasia** Coquillett

1 sp., *orichalcea* (Zetterstedt); boreal

27. Last section of M curved strongly forward and ending well before wing apex (Fig. 28). Aristal hairs shorter than basal diameter of arista. Prosternum haired .... **Synthesiomyia** Brauer & Bergenstamm

1 sp., *nudiseta* (Wulp); southern

Last section of M usually curved backward or only slightly forward, but if curved strongly forward and ending near or before wing apex, then aristal hairs several times as long as basal diameter of arista and prosternum bare 28

28. Presutural dorsocentral bristles long and very weak, scarcely distinguishable from the many long fine presutural hairs between and lateral to the dorsocentral rows .... ***Spilogona*** Schnabl, in part

see couplet 25

At least one presutural dorsocentral bristle strong and sharply differentiated from surrounding weak hairs, or all presutural dorsocentral bristles very short and stiff and scarcely distinguishable from surrounding short hairs 29

29. Presutural dorsocentral bristles very short and weak, scarcely distinguishable from surrounding hairs, the longest at most one-fourth as long as notopleural bristles. Head subquadrate in profile; antenna inserted very slightly below level of upper margin of eye (Fig. 6) .... ***Atherigona*** Rondani

1 sp., *orientalis* Schiner; southern

At least one presutural dorsocentral bristle moderately strong, clearly distinguishable from surrounding hairs, and at least half as long as notopleural bristles. Head variable in shape; antenna usually inserted well below level of upper margin of eye (Figs. 7–13) 30

30. Either anterior presutural dorsocentral bristle absent or weak and less than half as long as posterior *or* katepisternal bristles arranged in a nearly equilateral or isosceles triangle, with lower bristle almost equidistant from the two upper bristles; lower proepimeral bristle sometimes curved ventrally or anteroventrally (Fig. 20); anterior postsutural supra-alar bristle absent. Male frons at least one-fourth as wide as head (Figs. 7–10) 31

Anterior presutural dorsocentral bristle more than half as long as posterior, *and* katepisternal bristles, if more than two in number, with lower or lower posterior one closer to upper posterior one than to upper anterior one; lower proepimeral bristle curved dorsally; anterior postsutural supra-alar bristle present or absent. Male frons variable in width 44

31. Parafacial with a few fine hairs on upper third. Arista with longest hairs almost twice as long as width of first flagellomere .... ***Pentacricia*** Stein

1 sp., *aldrichii* Stein; widespread

Parafacial bare. Arista with longest hairs at most as long as width of first flagellomere 32

32. C ending just beyond apex of R$_{4+5}$ (Fig. 30) .... ***Allognota*** Pokorny

1 sp., *semivitta* Malloch; eastern

C ending at apex of M 33

33. Scutum with two pairs of postsutural dorsocentral bristles. Hind tibia with long posteroventral bristle at midlength .... ***Bithoracochaeta*** Stein

1 sp., *leucoprocta* (Wiedemann); southern

Scutum with three pairs of postsutural dorsocentral bristles. Hind tibia without posteroventral bristle 34

34. Frons with two pairs of reclinate orbital bristles, the anterior pair situated at about middle of frons and well before level of anterior ocellus; frons with two pairs of inclinate frontal bristles (Fig. 7) .... ***Caricea*** Robineau-Desvoidy

10 spp.; widespread; Malloch 1935 (as *Lispocephala* Pokorny)

Frons usually with one pair of reclinate orbital bristles or, if with two pairs, the anterior pair situated well behind middle of frons and little if at all before level of anterior ocellus; frons usually with at least three pairs of inclinate frontal bristles (Figs. 8–10) 35

35. Scutum usually with only one pair of presutural dorsocentral bristles; if a second anterior pair present, they are at most one-fifth as long as posterior pair 36

Scutum with two pairs of presutural dorsocentral bristles, the anterior pair at least one-third as long as posterior pair 37

36. Frons, at level of anterior ocellus, wider than its length from anterior ocellus to anterior margin (Fig. 8). Mid tibia with anteroventral bristle .... ***Schoenomyza*** Haliday

4 spp.; widespread; Huckett 1934

Frons usually longer than wide, but if as wide as long, mid tibia without anteroventral bristle .... ***Coenosia*** Meigen 41

37. Basal one-fourth or more of arista thickened; dorsum of pedicel depressed or flattened proximally (Fig. 14). Lower proepimeral bristle curved dorsally .... ***Tetramerinx*** Berg

9 spp.; widespread, on marine and lake shores; Huckett 1936 (as *Phyllogaster* Stein)

Arista thickened only at extreme base; dorsum of pedicel not depressed. Direction of lower proepimeral bristle variable 38

38. Legs black; hind tibia with two anterodorsal bristles 39

Fore and mid tibiae, and often most of legs, yellow; hind tibia usually with one anterodorsal bristle 40

39. Frontal vitta at level of anterior ocellus as wide in both sexes as distance between anterior pair of dorsocentral bristles; ocellar triangle densely silvery pruinose in male and whitish pruinose in female, extending to anterior margin of frons (Fig. 9) .... ***Limnospila*** **Schnabl**

1 sp., *albifrons* (Zetterstedt); widespread

Frontal vitta at level of anterior ocellus narrower in both sexes than distance between anterior pair of dorsocentral bristles; ocellar triangle not silvery nor whitish pruinose, and not extending to anterior margin of frons (Fig. 10) .... ***Pseudocoenosia*** **Stein**

4 spp.; boreal; Huckett 1936

40. Katepisternum with four bristles, three of which are situated on the posterior side of the triangle .... ***Macrorchis*** **Rondani**

3 spp.; widespread; Huckett 1936

Katepisternum with three bristles (Fig. 20) .... ***Coenosia*** **Meigen** 41

41. Hind femur with both a posterodorsal preapical bristle and a posterior preapical bristle (Fig. 43) .... ***Neodexiopsis*** **Malloch**

13 spp.; widespread; Huckett 1934, Snyder 1958

Hind femur with a posterodorsal preapical bristle but without a posterior preapical bristle 42

42. Hind tibia, near mid length, with an anterodorsal bristle and an anterior bristle but without an anteroventral bristle (Fig. 35) .... ***Coenosia*** **(*Coenosia* Meigen)**

2 spp.; widespread; Huckett 1934

Hind tibia, near mid length, with an anterodorsal bristle and usually with an anteroventral bristle but without an anterior bristle (Fig. 36) 43

43. Lower calypter not longer than broad, projecting at most very slightly beyond margin of upper calypter .... ***Coenosia*** **(*Oplogaster* Rondani)**

24 spp.; widespread; Huckett 1934

Lower calypter much longer than broad, with almost half its length or more projecting beyond margin of upper calypter .... ***Coenosia*** **(*Limosia* Robineau-Desvoidy)**

58 spp.; widespread; Huckett 1934

44. Parafacial with many fine hairs below level of lowest frontal bristle. Abdominal sternite 1 haired over most of its surface (Fig. 44) .... ***Lispoides*** **Malloch**

1 sp., *aequifrons* (Stein); widespread

Parafacial with few if any hairs below level of lowest frontal bristle. Abdominal sternite 1 bare or with a few posterior setae and hairs (Fig. 45) 45

45. Male 46

Female 56

46. Fore femur with a more or less distinct concavity on preapical part of ventral surface, and usually with one or two acute processes near base of concavity (Fig. 42); fore tibia either with a subbasal excavation on ventral surface (Fig. 42) or with dense shaggy black hairs in this area .... ***Hydrotaea*** **Robineau-Desvoidy, in part**

26 spp.; widespread; Huckett 1954

Fore femur without preapical ventral concavity; fore tibia without subbasal ventral excavation or shaggy black hairs on ventral surface 47

47. Hind tibia with a series of seven or more slender posterodorsal bristles on distal two-thirds, the bristles increasing more or less regularly in length toward apex of tibia (Fig. 38) .... ***Helina*** **Robineau-Desvoidy, in part**

60 spp.; widespread; Snyder 1949*a*

Hind tibia with at most five posterodorsal bristles, frequently with one or none; if more than one present, they are usually subequal in length 48

48. Hind tibia with three or more strong posterodorsal bristles that are more or less uniformly distributed along tibial length and are subequal in length and strength to anterodorsal bristles (Fig. 32) 49

Hind tibia usually with at most two strong posterodorsal bristles; if three or more present, they are restricted to basal half of tibia and are usually much shorter than anterodorsal bristles 51

49. Prosternum with a few fine hairs on posterior half (these hairs often very difficult to see) .... ***Helina*** Robineau-Desvoidy, in part
see couplet 47

Prosternum bare 50

50. Legs black. Hind tibia with posterodorsal bristles all subequal in length (Fig. 32) .... ***Drymeia*** Meigen, in part
see couplet 7

Either legs extensively yellow or hind tibia with posterodorsal bristles decreasing rather regularly in length toward its base (Fig. 36) .... ***Phaonia*** Robineau-Desvoidy, in part
see couplet 24

51. Hind tibia with a strong posterodorsal bristle at about one-half to two-thirds tibial length and sometimes with a shorter posterodorsal bristle basal to the stronger one (Figs. 33, 34) 52

Hind tibia without a strong posterodorsal bristle on apical half, with at most a few weak posterodorsal bristles that are either not longer than tibial diameter or are restricted to basal half of tibia (Figs. 40, 41) 55

52. Hind tibia with an apicoventral process bearing several strong bristles (Fig. 39) .... ***Hydrotaea*** Robineau-Desvoidy, in part
see couplet 46

Hind tibia with apex unmodified, or if modified, without strong bristles on process (Fig. 34) 53

53. Gena very narrow; lower margin of eye extending below level of major vibrissa (Fig. 11). Body blue black, shining. Legs black .... ***Hydrotaea*** Robineau-Desvoidy, in part
see couplet 46; Sabrosky 1949 (as *Ophyra* Robineau-Desvoidy)

Gena broader; lower margin of eye not extending below level of major vibrissa. Body variable in color, sometimes extensively yellow, but if entirely gray to black, then moderately pruinose. Legs sometimes extensively yellow 54

54. Gena anteriorly with one or two upcurved bristles that are distinctly stronger than other subvibrissal bristles; frontal bristles extending backward almost to level of anterior ocellus, with the upper bristle stronger than some of the preceding bristles (Fig. 13). One or more pairs of presutural acrostichal hairs bristle-like, almost as long as anterior pair of presutural dorsocentral bristles. Katepimeron bare .... ***Potamia*** Robineau-Desvoidy, in part
3 spp.; widespread; Snyder 1956 (as *Dendrophaonia* Malloch)

Gena anteriorly without upcurved bristles, or if bristles present, they are numerous and not stronger than other subvibrissal bristles; frontal bristles variable, often extending only two-thirds of distance from lunule to anterior ocellus and decreasing in length posteriorly, but sometimes with one or more long bristles near anterior ocellus. Presutural acrostichal hairs variable; sometimes one or more pairs bristle-like. Katepimeron bare or haired 60

55. Hind tibia with blunt apicoventral process and with three or more long weak posterodorsal bristles on basal half (Fig. 37) .... ***Drymeia*** Meigen, in part
see couplet 7

Hind tibia with apex unmodified and with at most very short posterodorsal bristles 64

56. Anteriormost orbital bristle proclinate or lateroclinate (Fig. 12) 57

Anteriormost orbital bristle reclinate 59

57. Hind tibia with three or more posterodorsal bristles more or less uniformly distributed along tibial length and subequal to anterodorsal bristles (Fig. 32) .... ***Drymeia*** Meigen, in part
see couplet 7

Hind tibia with at most two posterodorsal bristles that are restricted to apical half of tibia 58

58. Longest aristal hairs at least twice as long as basal diameter of arista (Fig. 13) .... ***Potamia*** Robineau-Desvoidy, in part

see couplet 54

Longest aristal hairs not longer than basal diameter of arista (Figs. 11, 12) .... ***Hydrotaea*** Robineau-Desvoidy, in part

see couplet 46

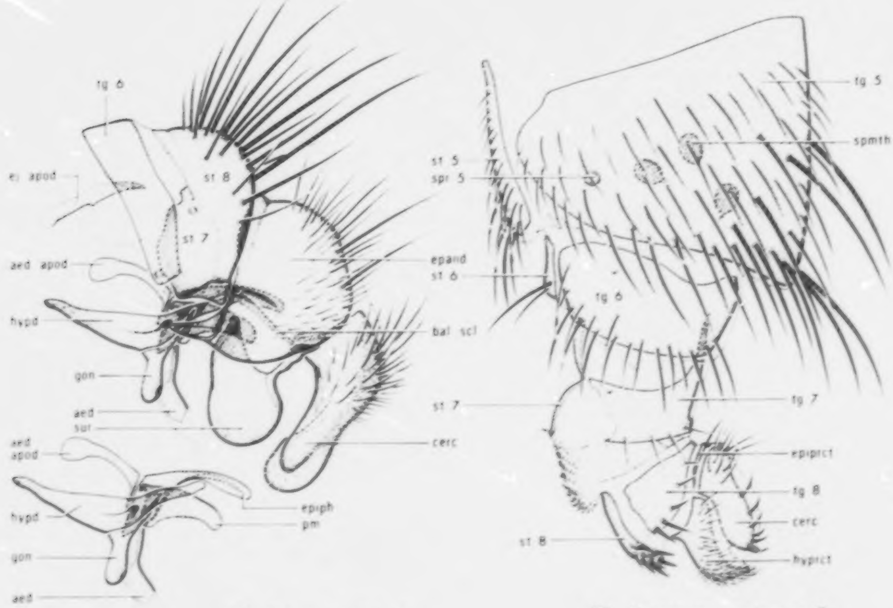
59. Hind tibia with a strong posterodorsal bristle, subequal to anterodorsal bristles, at or beyond midlength of tibia (Fig. 34), and sometimes with one or more rather strong posterodorsal bristles basal to the distal bristle (Fig. 33) 60

Hind tibia without posterodorsal bristles (Figs. 40, 41), or, if one or more bristles present, they are either much shorter and weaker than the anterodorsal bristles or are restricted to basal half of tibia 64

60. Anterior postsutural intra-alar bristle situated slightly behind level of supra-alar bristle. Last section of M curved at least slightly forward near wing margin (Fig. 29). Abdominal sternite 1 haired .... ***Muscina*** Robineau-Desvoidy

7 spp.; widespread; Snyder 1956

Anterior postsutural intra-alar bristle situated at or in front of level of supra-alar bristle. Last section of M rarely curved forward. Abdominal sternite 1 bare or haired 61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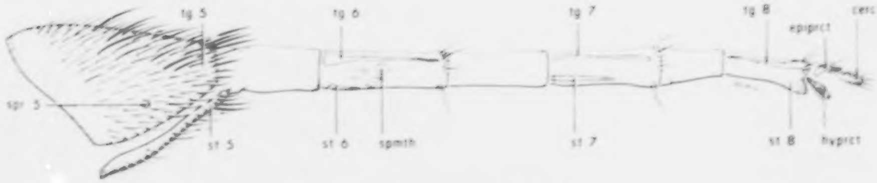
47 Helina evecta ♂ **48** Hebecnema umbratica ♀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hyprct

49 Helina evecta ♀

Figs. 105.47–49. Terminalia: (47) male terminalia of *Helina evecta* (Harris) in left lateral view; female terminalia of (48) *Hebecnema umbratica* (Meigen) and (49) *Helina evecta* in left lateral view.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; bac scl, bacilliform sclerite; cerc, cercus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; st, sternite; spmth, spermatheca; spr, spiracle; sur, surstylus; tg, tergite.

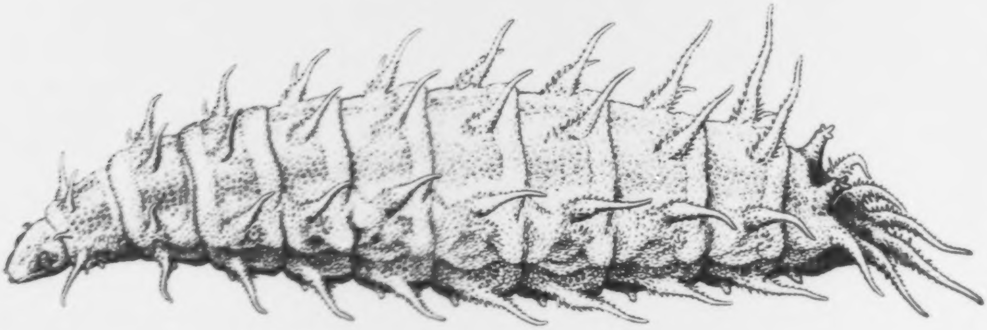
61. Prosternum broadened anteriorly, separated from proepisternum by less than its greatest width (Fig. 18). Anterior postsutural supra-alar bristle much shorter than posterior notopleural bristle. Aristal hairs shorter than basal diameter of arista .... ***Lophosceles*** Ringdahl
5 spp.; boreal and alpine

Prosternum parallel-sided or nearly so, separated from proepisternum by more than its greatest width (Fig. 19). Anterior postsutural supra-alar bristle shorter or longer than posterior notopleural bristle. Aristal hairs sometimes longer than basal diameter of arista 62

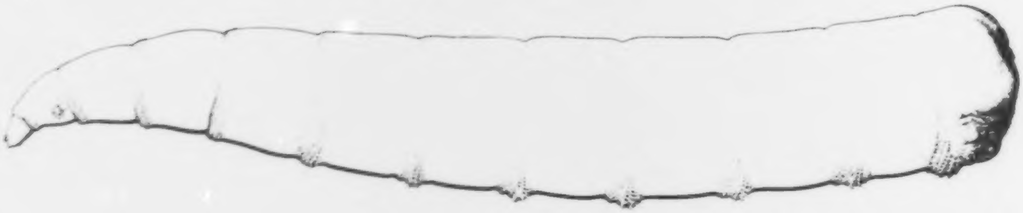
62. Prosternum with a few fine hairs on at least posterior half (often difficult to see) 63

Prosternum bare .... ***Phaonia*** Robineau-Desvoidy, in part
see couplets 24, 47; the female of *Helina luteisquama* (Zetterstedt) also keys out here

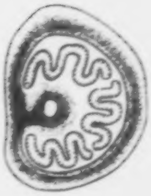
63. Hind tibia with three or more strong posterodorsal bristles .... ***Helina*** Robineau-Desvoidy, in part
see couplet 47



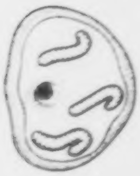
50 Fannia canicularis



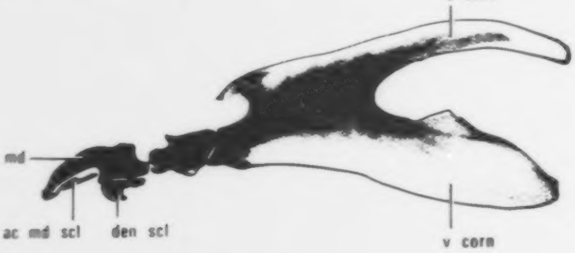
51 Potamia sp.



52 Musca domestica



53 Potamia sp.



54 Potamia sp.

Figs. 105.50–54. Larvae: (50) *Fannia canicularis* (Linnaeus) in lateral view; (51) *Potamia* sp. in lateral view; posterior spiracle of (52) *Musca domestica* Linnaeus and (53) *Potamia* sp.; (54) cephalopharyngeal skeleton of *Potamia* sp.

Abbreviations: ac md scl, accessory mandibular sclerite; d corn, dorsal cornu; den scl, dental sclerite; md, mandible; v corn, ventral cornu.

Hind tibia with one strong posterodorsal bristle at about five-sevenths tibial length (Fig. 34) .... ***Phaonia*** Robineau-Desvoidy, in part
see couplet 24

64. Hind tibia with a very weak anterodorsal preapical bristle (Fig. 40). Abdominal sternite 1 with strong hairs on posterior margin (Fig. 46) .... ***Brontaea*** Kowarz
4 spp.; widespread

Hind tibia with a strong anterodorsal preapical bristle (Fig. 41). Abdominal sternite 1 bare or with fine weak hairs 65

65. Anterior postsutural supra-alar bristle short to very long but clearly distinguishable from surrounding hairs .... ***Helina*** Robineau-Desvoidy, in part
see couplet 47

Anterior postsutural supra-alar bristle absent or indistinguishable 66

66. Arista pubescent, the longest hairs not longer than basal diameter of arista. Femora and tibiae entirely dark .... ***Spilogona*** Schnabl, in part
see couplet 25

Either arista plumose with longest hairs at least twice as long as basal diameter of arista, or tibiae (and often femora) extensively yellow 67

67. Hind tibia with one anterodorsal bristle 68

Hind tibia with two or more anterodorsal bristles (Fig. 41) 69

68. Crossveins unclouded. Katepimeron and meron bare. Ovipositor short, usually extensively exposed in dry specimens, with short broad sclerites and often with spinose bristles (Fig. 48) .... ***Hebecnema*** Schnabl
5 spp.; widespread; Malloch 1921*b*

Crossveins at least faintly clouded. Katepimeron and meron sometimes with fine hairs. Ovipositor long and slender, usually retracted into pregenital segments with at most the slender cerci exposed, and without spinose bristles (Fig. 49) ..... ***Helina*** Robineau-Desvoidy, in part
see couplet 47

69. Arista plumose, the longest hairs at least twice as long as basal diameter of arista .... ***Helina*** Robineau-Desvoidy, in part
see couplet 47

Arista pubescent, the longest hairs not longer than basal diameter of arista .... ***Helina*** Robineau-Desvoidy, in part
see couplets 25, 47 ***Spilogona*** Schnabl, in part

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CALLIPHORIDAE

106

G. E. SHEWELL

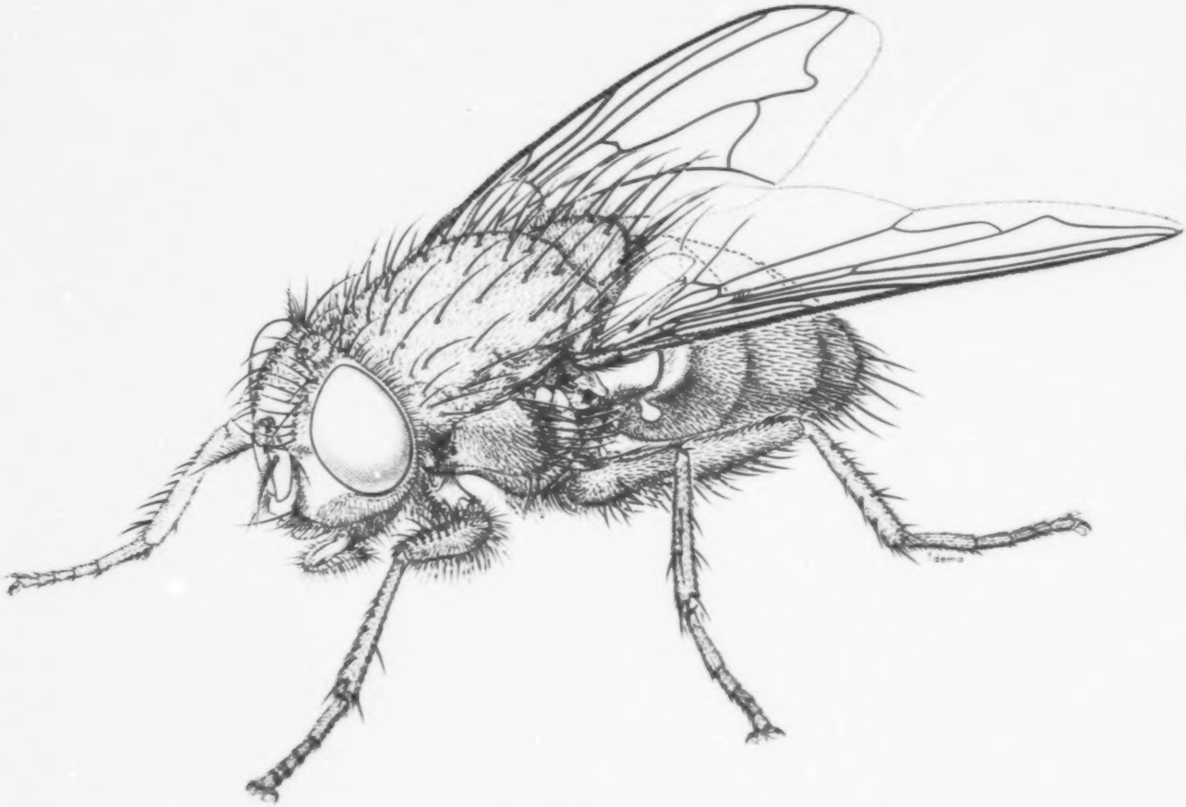

Fig. 106.1. Female of *Calliphora terraenovae* Macquart.

Mostly robust medium-sized to large flies (Fig. 1), partly or wholly metallic blue or green, sometimes polished black or dull brassy, occasionally small, slender, and without metallic sheen. Male seldom holoptic; upper facets of eye not much enlarged, but with frons always narrower than in female, and lacking orbital and outer vertical setae. Sexes sometimes with differing leg chaetotaxy, occasionally with marked difference in body color. Length 4.0–16.0 mm.

Adult. Head: wider than high, in profile about half to nearly three-fourths as long as high (Figs. 2–5). Frons more or less sloping, rarely prominent; antennal axis equal to or less than vibrissal axis; lunule exposed, bare, shining; frontal setae reaching pedicel; fronto-orbital plate and margin of frontal vitta usually with fine, often numerous, long hairs (Fig. 7); female with one reclinate orbital seta above, and two proclinate orbital setae outside frontal row; weak supplementary ocellar setae often present; postocellar and paravertical setae often weak; paravertical setae absent in Rhiniini; parafacial usually haired; vibrissa strong. Genal groove large, usually bare; facial ridge haired on at least lower half, rarely setose; gena thickly haired, seldom less than one-fourth height of eye, often much broader; ventral margin in profile usually straight with well-formed vibrissal angle (Figs. 2–4) but sometimes rounded into facial plane; postgena usually well-developed. Postcranium convex below, flat or shallowly concave above. Intrapostocular setulae (between eye margin and postocular row) usually present, sometimes very pale and fine. Antennal scape very short, flush with lunule; pedicel short; first flagellomere two to six times as long as pedicel, often more inflated in female; arista about as long as antenna, long plumose on at least basal two-thirds, rarely pubescent or pectinate. Proboscis short; labella fleshy; palpus normal, slightly clavate, rarely very short filiform (Fig. 2), usually yellow.

Thorax: middle of propleuron, prosternum, postalar wall, and metasternal area usually haired; infrasquamal hairs present; setae strong; presutural and postsutural series on scutum each with two or three setae, sometimes reduced or absent anteriorly; two to five postpronotal setae present; anterior presutural supra-alar (outer posthumeral) seta sometimes absent (Fig. 21), when present close to notopleural margin (Fig. 22); two notopleural setae present, with the anterior one sometimes stronger; one to three lateral scutellar setae present, often with weaker supplementaries (Figs. 24–27); apical scutellar setae usually strong; proepisternal and proepimeral setae present, often with one or two weaker supplementaries; seven to ten anepisternal setae present, the upper two shorter and declinate; anepimeron haired, sometimes with a few weak setae above; katepisternal setae usually arranged 2:1, rarely 1:1 or 1:2. Greater ampulla reniform. Coxopleural streak present or absent. Spiracles usually large; anterior one covering most of its sclerite; posterior one oval, with anterior valve plate usually larger than posterior valve plate, sometimes with ventral fringe of fine hairs overlying anterior one. Small subscutellum rarely developed.

Wing root often weakly haired in tympanic pit and on anterior part of suprasquamal ridge; this ridge sometimes with a conspicuous cluster of setae posteriorly (Fig. 14). Calypteres often haired on dorsal or ventral surfaces (Figs. 12, 15). Basal part of R (stem vein) sometimes ciliate above (Figs. 13, 15); subcostal sclerite sometimes setose (Fig. 17); R_{4+5} usually with hairs or spinules on node above, and with a few hairs beyond. Costal spine rarely developed. Bend of M without trace of extension (stump vein) except in Phormiini; curvature usually abrupt, right-angled or acute, uneven beyond bend, sometimes more gently rounded, with obtuse angle and evenly curved apical part (Figs. 8–10, 18–20). Cell r_{4+5} usually open, rarely closed in margin.

Legs moderately robust. Male claws sometimes elongate, seldom conspicuously so. Other sexual differences limited to slight variation in chaetotaxy, especially of middle leg. Fore femur with posterodorsal and posteroventral rows of setae, and with partial second posterodorsal row. Mid femur usually with anteroventral and posteroventral rows of two to six setae on basal half, rarely with posteroventral row to apex, anteriorly with short row at middle and sometimes a preapical seta, posteriorly with diagonal row of three setae near apex. Hind femur with complete anterodorsal and incomplete or uneven anteroventral rows, with the posteroventral row confined to basal half. Fore tibia with anterodorsal row of setae always extending beyond middle, usually with one posterior seta; apical anteroventral seta absent; apical posterodorsal seta weak or absent. Mid tibia with one to three anterodorsal setae; usually one posterodorsal and two posterior setae present, with the lower one of the latter lying very close to the posterodorsal one; one or two ventral setae present; apical posterodorsal seta weak or absent; other apical setae strong. Hind tibia with anterodorsal row of three to six setae or with more numerous short setae forming ciliation, with two anteroventral and two to five posterodorsal setae, and sometimes also with a strong apical posterodorsal seta.

Abdomen: with five segments preceding terminalia and with three or four segments comprising terminalia. Tergites 1–5 large; tergites 1 and 2 combined. Sternites narrow, exposed or slightly overlapped laterally; sternite 5 strongly bilobate in male. Spiracles 1–5 usually small, bare, rarely very large with dense erect marginal pile (*Boreellus* Aldrich & Shannon), enclosed in tergites at or near ventral margins.

Female usually oviparous. Terminalia (Figs. 33–37) long, slender, tubular, normally retracted within segment 5. Segments 6–8 mostly membranous, with long narrow sternites and more complex often subdivided tergites. Epiproct and hypoproct short, blunt. Cercus short. Spiracles 6 and 7 usually in tergite 6, or just below it (Figs. 35, 39); rarely spiracle 6 situated in membrane behind tergite 5 (*Opsodexia* Townsend). Note: *Bellardia* Robineau-Desvoidy is viviparous, with short terminalia (Figs. 38, 39).

Male terminalia (Figs. 28–32) usually small, enclosed within tergite 5, sometimes large and exposed. Tergite 6 short and narrow; sternite 6 a bare U-shaped plate with arm of left side longer; spiracle 6 situated in membrane laterally, close to next segment. Syntergosternite 7 + 8 a strongly arched dorsal plate enclosing spiracle 7 laterally, sometimes with partial intersegmental grooves. Epandrium smaller. Cerci rigid, forcipate; articulated surstylus sclerotized, about as long as cercus; sometimes cerci vestigial with surstyli long and forcipate (*Cynomya* Robineau-Desvoidy); sternite 10 in form of slender lateral rods (bacilliform sclerites), or sometimes a narrow median plate (Angioneurini); hypandrium simple, with long apodeme; gonopod fused to its lateral margin; paramere slender and free-moving; aedeagus with short sclerotized basiphallus (phallotheca) and more or less elongate membranous distiphallus; aedeagal apodeme rodlike; basiphallus with slender epiphallus projecting posteriorly; distiphallus usually with enlarged basal part (hypophallus) and slender tubular apex (acrophallus, juxta); sclerotization of basiphallus extended along posterior surface of distiphallus, dividing and curving anteriorly in two slender dorsolateral processes (paraphalli); hypophallus and acrophallus usually microdenticulate or partially sclerotized; ejaculatory apodeme usually large, flabelliform, and lying in epandrial cavity.

Egg. Length 0.9–1.5 mm; width 0.3–0.4 mm; color shining white, darkening with age to grayish; shape elongate ovoid, slightly arcuate, in lateral view flat or slightly concave dorsally and convex ventrally. Chorion with faint reticulate pattern. A narrow, slightly sunken plastron area along middorsal line bounded by more or less parallel ridges marking hatching lines that run from micropyle to near posterior pole.

Larva. Pale yellow to white, cylindrical, tapered anteriorly, usually over five times longer than broad. Segments, except first, with more or less complete bands of small reclinate spines anteriorly; last five or more segments with bands of proclinate spines posteroventrally; rarely cuticle evenly convered with prominent reclinate spines (*Protocalliphora* Hough). Cephalopharyngeal skeleton well-developed, with strong paired mandibular hooks.

First instar (Figs. 42–49) less than 2 mm long, usually with blunt-tipped labrum (hatching spine) between rudimentary mandibular hooks; sometimes with strong hooked mandibles and with labrum vestigial or absent (*Protocalliphora*, *Bellardia*), rarely with large hooked labrum and vestigial mandibles

(*Pollenia* Robineau-Desvoidy). Anterior spiracle absent; posterior spiracle bilobate, without peritreme; spiracular disc sometimes partly fringed with fine hairs.

Second instar (Fig. 50) 2–9 mm long, similar to third instar, but with cephalopharyngeal skeleton relatively weak and posterior spiracle with only two openings.

Third instar (Figs. 40, 41, 51–54) 9–22 mm long. Mandibles large, sharply hooked, sometimes with accessory oral (labial) sclerite between their tips (Fig. 41); dorsal cornu of tentoropharyngeal sclerite without window. Anterior spiracle with short flattened stalk bearing 4–12 nodular branches arranged fan-wise; posterior spiracular plate with three straight subparallel openings aligned diagonally and encircled by dark peritreme; ecdysial scar usually distinct (Fig. 54); spiracular disc flat, surrounded by 12–14 more or less prominent tubercles (Fig. 53). Anus in rounded posteroventral protuberance bearing short lateral papillae.

Biology and behavior. Most female Calliphoridae are oviparous, including all those most familiar to humans. The common species called bluebottles or greenbottles (Calliphorini, Luciliini) oviposit indoors on fresh or cooked meats, fish, or dairy products, and in the open on carcasses of all kinds. Some of the same species are also attracted to excrement and thus can be transmitters of enteric pathogens. Probably most damaging in economic terms are the blow flies whose larvae are called screwworms (Chrysomyiini, Phormiini, Luciliini). Females of this group lay eggs on fresh skin lesions or on soiled wool, especially around orifices of domestic animals, and the maggots inflict gross wounds by burrowing in healthy tissue. Cattle and sheep on open ranges are frequently attacked, and losses are severe enough to warrant expensive control measures, especially against the primary screwworm *Cochliomyia hominivorax* (Coquerel) (Bushland 1960, Norris 1965). In the tropics and subtropics, this species is also an important pest of humans (James 1947). Females of *Protocalliphora* oviposit in the nests of various birds, including swallows. The larvae attach themselves to the skin of the nestlings and suck blood. Although such infestations can be severe, their effect on the population of beneficial birds is difficult to assess (Johnson 1929, Hall 1948). Screwworms (*Bufolucilia* Townsend) also infest toads, frogs, and salamanders, with in most cases fatal results. Adults of the cluster fly, *Pollenia* spp., cause much annoyance by entering heated dwellings in the fall, often in great numbers, to hibernate. Most of them cannot escape from the houses the following spring, and either die by the hundreds in attics or else find their way down into the lower rooms. The accumulation of dead flies attracts dermestid beetles and other household pests. Eggs of the cluster fly are laid on soil, and the larvae feed on earthworms (Yahnke and George 1972). A small tribe, Angioneurini[1] (Enderlein 1928, Angioneurinae), of muscid-like blow flies are internal parasites of land snails (Reinhard 1929). No native calliphorids are known to be viviparous, but two European species were apparently introduced into the United States many years ago, and one, *Bellardia agilis* (Meigen), is established in New Jersey and perhaps adjoining states. The larva (Figs. 46, 49) is probably parasitic on an introduced European earthworm. Adult calliphorids visit flowers or rest on low foliage, usually in bright sunlight. The sound of their buzzing, when loud and continuous, usually indicates the presence of carrion in the vicinity. Laboratory colonies of common blow flies are comparatively easy to maintain, and they are frequently used as test animals in both basic and applied research. The definitive work on North American blow flies is that of Hall (1948). This monograph, though primarily taxonomic, contains much information on the synanthropic role of the group and on control measures. It illustrates the larval stages, summarizes biological data for most species, and includes a list of biological references (with titles omitted). The medical aspect of blow fly ecology is broadly treated in James (1947), a work that also contains biological data on several Nearctic species and includes perhaps all the more important references in the medical literature. Later taxonomic treatments are those of James (1955) on the California fauna, and of Hall and Townsend (1977) on the species of Virginia. The latter has an updated bibliography. Contributions to larval taxonomy and biology are those of Laake *et al.* (1936), Knipling (1936, 1939), Menees (1962), and Thompson and Davies (1973–1974).

Classification and distribution. Blow fly classification is conservative, reflecting the need for stability in a group that has a significant impact on human society. Compared with other Calyptratae, the taxonomy is less dependent on chaetotaxy, hardly at all on immature stages, and until recently, very little on terminalia above the species level. Some important group characters of the vestiture on and around the base of the wing have long defined the three main divisions, based on *Calliphora* Robineau-Desvoidy, *Chrysomya* Robineau-Desvoidy, and *Rhinia* Robineau-Desvoidy, regardless of whether the family name is used in a restricted sense (most American authors), or expanded to include Sarcophagidae (many Old World authors). Within these divisions are long-established subgroups associated with *Phormia* Robineau-Desvoidy, *Pollenia*, and *Lucilia* Robineau-Desvoidy, although the first two have also been given higher rank (Shannon 1926, Hall 1948). The status of peripheral genera such as *Bengalia* Robineau-Desvoidy, *Eggisops* Rondani, and *Mesembrinella* Giglio-Tos has mostly been in doubt even when it became no longer possible to include them in Tachinidae.

In a recent paper on the world fauna, Lehrer (1970) has examined the aedeagus in detail, finding a correlation between its length and the distance of its epiphallus from the base. He theorizes that some blow fly phylogeny has involved a gradual increase of aedeagal length, though without suggesting any selective advantage for this, nor attempting to relate it to changes in the female genital structure. His classification recognizes 22 tribes in nine subfamilies and proposes both a restricted and an overall concept for the family name. Many of Lehrer's groups fall outside the scope of our fauna. His new tribes Boreellini, Protocalliphorini, Hemiluciliini, Cochliomyiini, and Acrophagini, with the exception of the last named, do not substantially alter generic relationships, but involve further splitting of already small groups of genera. Their purpose could be served equally within the present classification by the use of subtribes. The case of Acrophagini is more complex, as it involves rearranging the difficult tribe Calliphorini. It presents the uncertain application of a restricted orthogenesis (gradual lengthening of the aedeagus) in a holometabolous group that displays heterochronous (both oviparous and viviparous) development (Reeve and Huxley 1945). In Calliphoridae, viviparity seems to have reached the generic level, which perhaps places the family in an intermediate position between the Muscidae, where it occurs in isolated species (e.g. *Musca*), and Sarcophagidae in which it is universal. A discussion by Schumann (1973) of the taxonomic history of several viviparous genera of Calliphoridae is relevant to the work of Lehrer, who seems to have misjudged the extent of viviparity in this group, and whose tribe Acrophagini is in part based on a misidentification of the female of the oviparous species *Acrophaga subalpina* Ringdahl (Lehrer 1972). Fourteen viviparous genera in five tribes are now known in blow flies, not including the Neotropical Mesembrinellinae, which Guimaraes (1977) has accorded family status. The genera *Opsodexia* and *Angioneura* Brauer & Bergenstamm (=*Opelousia* Townsend) belong to the tribe Angioneurini. Downes (1965) placed both as subgenera of *Melanomya* Rondani in the tribe Melanomyini. *Angioneura* and *Melanomya* have been tentatively assigned to the family Rhinophoridae (Crosskey 1977) although both lack a coxopleural streak. Species of *Angioneura* have been reared from snails of the genus *Succinia*. The first-instar larva resembles that of *Eggisops pecchiolii* Rondani (Thompson 1921) in having a strong upcurved hooked labrum firmly fused to the tentoropharyngeal sclerite, as well as a strong pair of downcurved moveable mandibles (unpublished data). Although *Eggisops* is larviparous and *Angioneura* oviparous, they are both parasitic in land snails. Together with *Melinda* Robineau-Desvoidy, another oviparous snail parasite with a similar larva (Keilin 1919), the three genera probably form a monophyletic tribal group. *Melanomya*, although apparently rather common in Europe, has not been reared and its affinity is still doubtful. Townsend (1935) believed that the important plesiomorphic characters resided in the female reproductive system, whereas the male system had the most apomorphic value. He stressed the importance of larval taxonomy, correctly observing that adaptive features appear as early as the first instar (Figs. 42–49). An improved classification for the Calliphoridae clearly depends on much greater knowledge than we now have of the immature stages.

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[1] Cited in error as Opsodexiinae in Vol. 1, p. 104.

Blow flies are distributed world wide, from the northern limit of land to New Zealand and the subantarctic islands. Over 1000 species in about 150 genera are recognized, more than four-fifths of the species and three-fifths of the genera being restricted to the Old World. The Afrotropical region has the richest fauna with about 300 species in 40 genera, nearly half of them belonging to the Rhiniini. This distinctive tribe, which most authors accord subfamily rank, has no endemic New World species. The presence of a common and widespread rhiniine fly in Bermuda is best explained as an accidental introduction. The poverty of the New World fauna is remarkable, especially in the Neotropical region, for which James (1970) lists less than 100 valid species. Within the last decade several species of the Old World tropical and subtropical genus *Chrysomya* have been introduced into South and Central America and become established, spreading as far as the southwestern United States (Baumgartner and Greenberg 1984).

The fossil record for this family is fragmentary, consisting of late Cretaceous puparial remains (McAlpine 1970), puparia of *Cochliomyia macellaria* (Fabricius) associated with an avian bone fragment of Pleistocene age (Gagné and Miller 1982), and empty puparia from a *Megatherium* skull (possibly Pleistocene), concerning which a paper was planned but apparently never published (James 1970). Puparia of recent species of blow flies are also found from time to time during excavation of prehistoric burial sites (Teskey and Turnbull 1979).

Key to genera

1. Basal section of R (stem vein) ciliate on posterodorsal surface (Figs. 13, 15) .... CHRYSOMYIINAE....2

Basal section of R bare (Fig. 14) .... CALLIPHORINAE....9

2. Posterior margin of hind coxa haired. Gena yellow or orange, with mostly yellow hairs ... . CHRYSOMYIINI....3

Posterior margin of hind coxa bare or with a few hairs on lateral corner only. Gena black 5

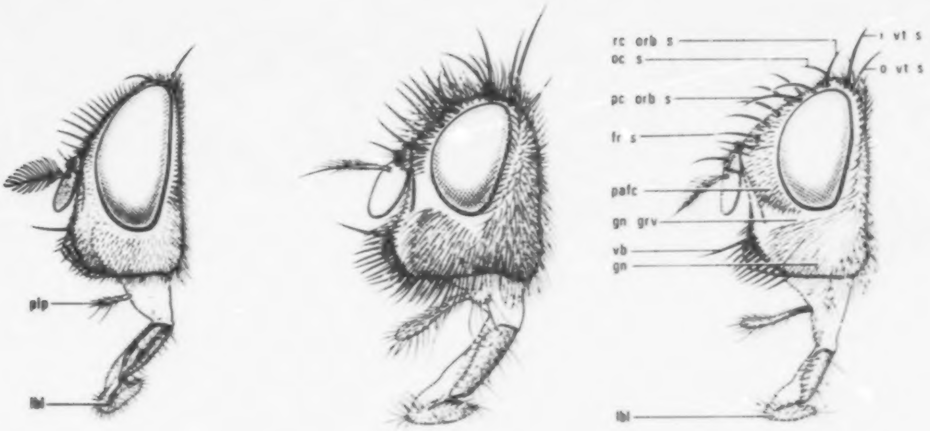
3. Mesonotum with distinct dark vittae. Lower calypter haired above (Fig. 15); wing clear along C 4

Mesonotum not distinctly vittate. Lower calypter bare above; wing clouded along C (Fig. 18) .... ***Chloroprocta*** Wulp

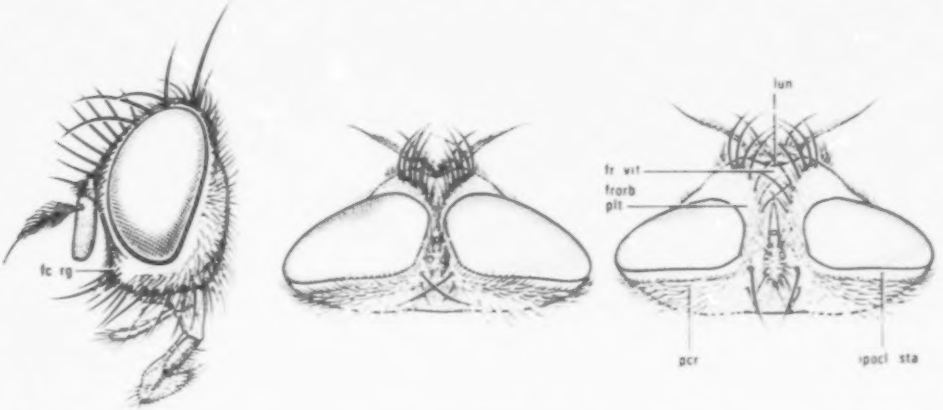
1 sp., *fuscanipennis* (Macquart); Texas

4. Hairs pale on posterior margin of hind coxa and on first abdominal sternite. Palpus filiform (Fig. 2) .... ***Cochliomyia*** Townsend

4 spp.; U.S.A., southern Ontario; Hall 1948


plp
lbl
rc orb s
oc s
i vt s
o vt s
pc orb s
fr s
pafc
gn grv
vb
gn
lbl

2 Cochliomyia macellaria ♂ **3** Boreellus atriceps ♀ **4** Pollenia sp. ♀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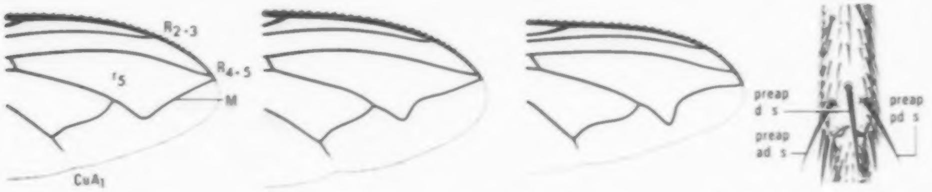
5 Opsodexia serva ♀ **6** Calliphora terraenovae ♂ **7** Cynomya cadaverina ♂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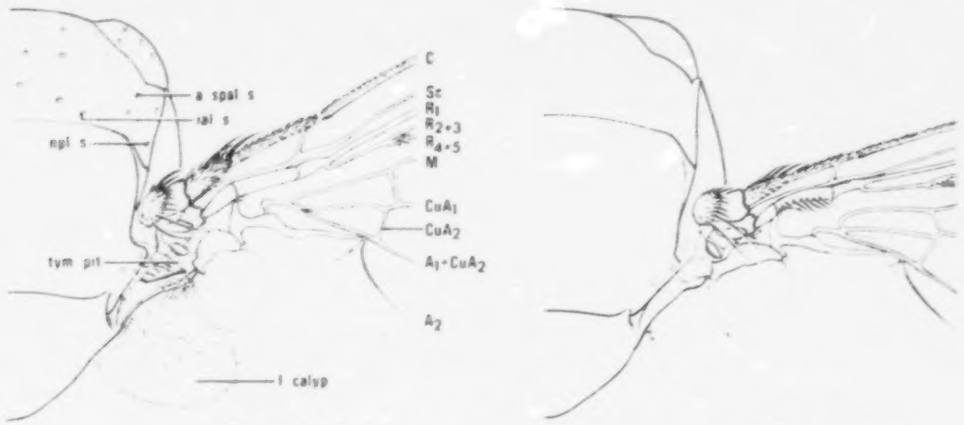
preap d s
preap ad s
preap pd s

8 Bellardia agilis ♂ **9** Acrophaga genarum ♀ **10** Calliphora vomitoria ♀ **11** Melanodexia grandis ♀

Figs. 106.2–11. Heads, wings, and leg: lateral views of heads of (2) *Cochliomyia macellaria* (Fabricius), (3) *Boreellus atriceps* (Zetterstedt), (4) *Pollenia* sp., and (5) *Opsodexia serva* (Walker); dorsal views of heads of males of (6) *Calliphora terraenovae* Macquart and (7) *Cynomya cadaverina* Robineau-Desvoidy; wing tips of (8) *Bellardia agilis* (Meigen), (9) *Acrophaga genarum* (Zetterstedt), and (10) *Calliphora vomitoria* (Linnaeus); (11) dorsal view of apex of left hind tibia of *Melanodexia grandis* Shannon.

Abbreviations: fc rg, facial ridge; frorb plt, fronto-orbital plate; fr s, frontal seta; fr vit, frontal vitta; gn, gena; gn grv, genal groove; ipocl sta, intrapostocular setula; i vt s, inner vertical seta; lbl, labellum; lun, lunule; oc s, ocellar seta; o vt s, outer vertical seta; pafc, parafacial; pc orb s, proclinate orbital seta; pcr, postcranium; plp, palpus; preap ad s, preapical anterodorsal seta; preap d s, preapical dorsal seta; preap pd s, preapical posterodorsal seta; rc orb s, reclinate orbital seta; vb, vibrissa.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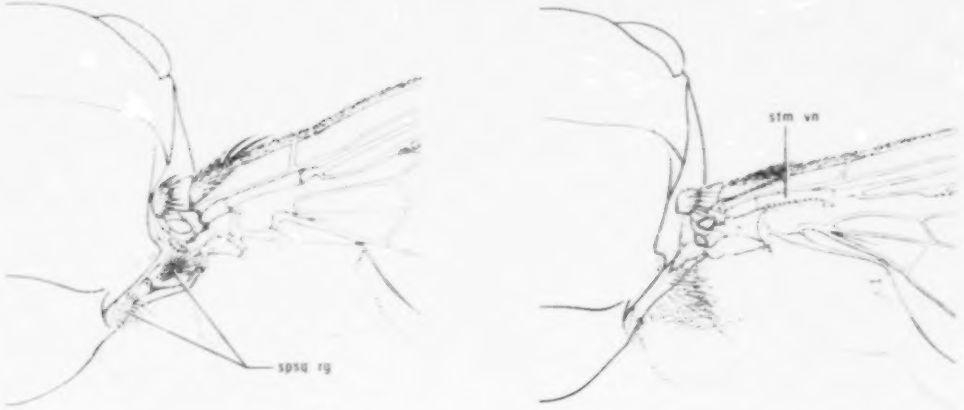
A1+CuA2
A2

12 Calliphora sp. ♀

13 Phormia regina ♀


spsq rg
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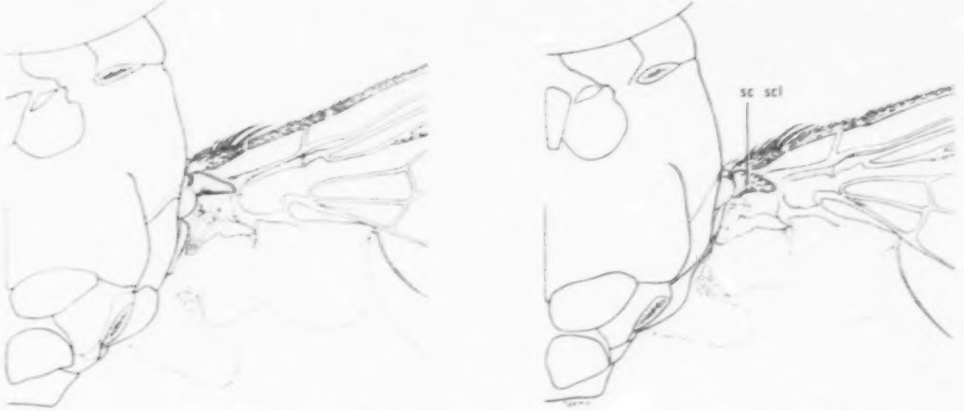
14 Phaenicia sericata ♀

15 Paralucilia wheeleri ♀

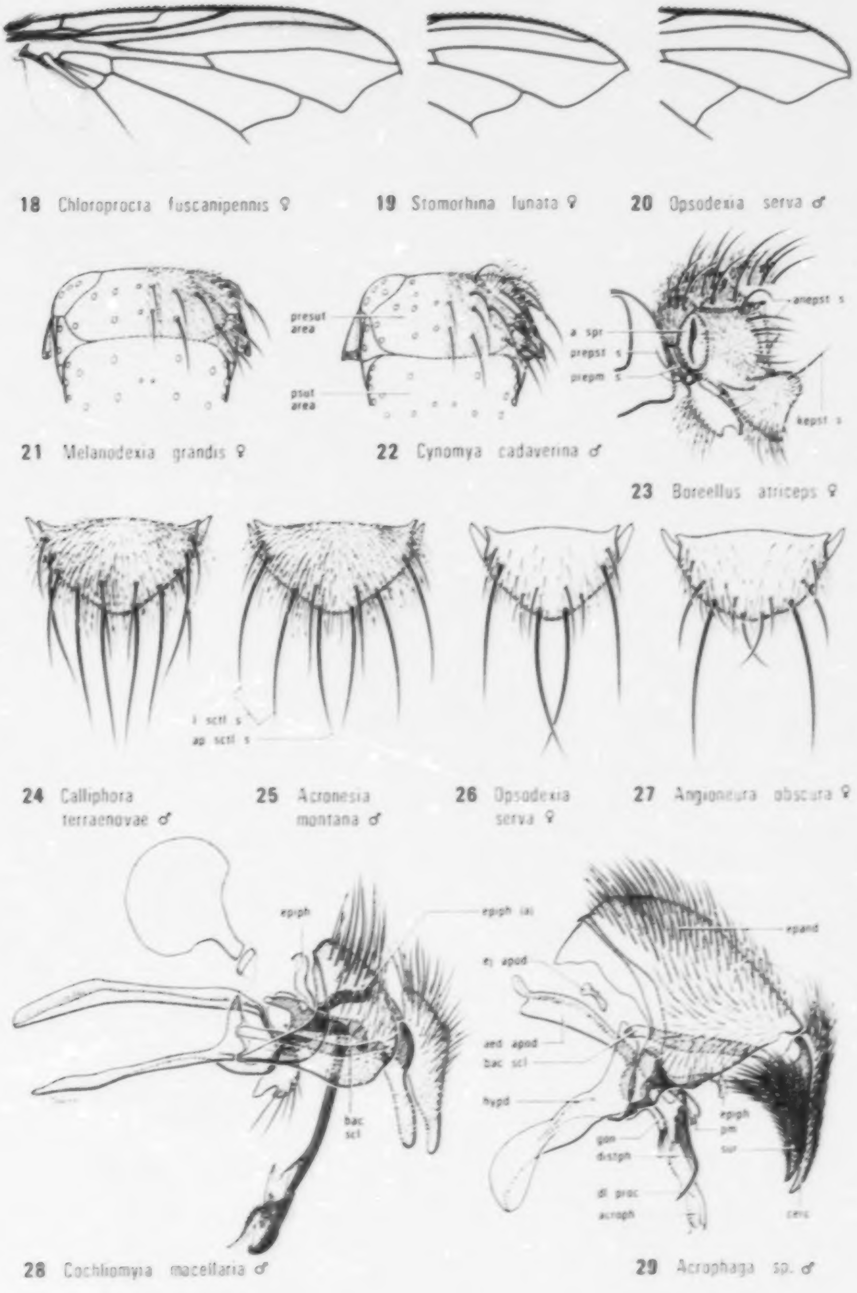


16 Phaenicia sericata ♀

17 Lucilia illustris ♀

Figs. 106.12–17. Bases of wings: dorsal views of (12) *Calliphora* sp., with thoracic chaetotaxy, (13) *Phormia regina* (Meigen), (14) *Phaenicia sericata* (Meigen), and (15) *Paralucilia wheeleri* (Hough); ventral views of (16) *Phaenicia sericata* and (17) *Lucilia illustris* (Meigen).

Abbreviations: a spal s, anterior supra-alar seta; ial s, intra-alar seta; l calyp, lower calypter; npl s, notopleural seta; sc scl, subcostal sclerite; spsq rg, suprasquamal ridge; stm vn, stem vein; tym pit, tympanic pit.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18 Chloroprocta fuscanipennis ♀ **19** Stomorhina lunata ♀ **20** Opsodexia serva ♂

21 Melanodexia grandis ♀ **22** Cynomya cadaverina ♂ **23** Boreellus atriceps ♀

24 Calliphora terraenovae ♂ **25** Acronesia montana ♂ **26** Opsodexia serva ♀ **27** Angioneura obscura ♀

28 Cochliomyia macellaria ♂ **29** Acrophaga sp. ♂

Figs. 106.18–29. Wings, thoraces, and male terminalia: (18) wing of *Chloroprocta fuscanipennis* (Macquart); wing tips of (19) *Stomorhina lunata* (Fabricius) and (20) *Opsodexia serva* (Walker); dorsal views of anterior part of thorax of (21) *Melanodexia grandis* Shannon and (22) *Cynomya cadaverina* Robineau-Desvoidy; (23) anterior pleural region of *Boreellus atriceps* (Zetterstedt); scutellum of (24) *Calliphora terraenovae* Macquart, (25) *Acronesia montana* (Shannon), (26) *Opsodexia serva*, and (27) *Angioneura obscura* (Townsend); male terminalia of (28) *Cochliomyia macellaria* (Fabricius) and (29) *Acrophaga* sp.

Abbreviations: acroph, acrophallus; aed apod, aedeagal apodeme; anepst s, anepisternal seta; ap sctl s, apical scutellar seta; a spr, anterior (mesothoracic) spiracle; bac scl, bacilliform sclerite; cerc, cercus; distph, distiphallus; dl proc, dorsolateral process (paraphallus); ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; epiph (a), alternate position of epiphallus; gon, gonopod; hypd, hypandrium; kepst s, katepisternal seta; l sctl s, lateral scutellar seta; pm, paramere; prepm s, proepimeral seta; prepst s, proepisternal seta; presut, presutural; psut, postsutural; sur, surstylus.

These hairs black. Palpus clavate .... ***Paralucilia*** Brauer & Bergenstamm
1 sp., *wheeleri* (Hough); western U.S.A.

5. Lower facial margin not produced strongly beyond vibrissae (Fig. 3). Hairs of gena black. Section of M beyond bend concave on outer side .... PHORMIINI....6

Lower facial margin strongly produced. Hairs of gena pale. Section of M beyond bend straight or convex on outer side (Fig. 19) .... RHINIINI.... ***Stomorhina*** Rondani
1 sp., *lunata* (Fabricius); immigrant to Bermuda

6. Upper calypter bare above .... ***Protocalliphora*** Hough
11 spp.; widespread

Upper calypter sparsely pilose above[2] 7

7. Anterior spiracle mostly orange yellow. Upper calypter pale, with pale pile. Presutural acrostichal setae weak .... ***Phormia*** Robineau-Desvoidy
1 sp., *regina* (Meigen); widespread, temperate

Anterior spiracle black. Upper calypter with dark border and dark pile. Presutural acrostichal setae absent 8

8. Hairs of abdominal dorsum erect. Anterior spiracle much enlarged, with its horizontal axis almost equal to length of first antennal flagellomere (Fig. 23) ... ***Boreellus*** Aldrich & Shannon
1 sp., *atriceps* (Zetterstedt); Arctic

Hairs of abdominal dorsum decumbent except on segment 5. Anterior spiracle normal .... ***Protophormia*** Townsend
1 sp., *terraenovae* (Robineau-Desvoidy); widespread, boreal

9. Middle of propleuron bare, or if haired, then body not metallic blue or green 10

Middle of propleuron haired. Body partly or wholly shining metallic blue or green 13

10. Gena about half height of eye. Parafacial haired to lower eye margin, seldom less than half width of face at middle; face descending well below vibrissa (Fig. 4) .... POLLENIINI....11

Gena about one-fourth height of eye. Parafacial bare on lower half or more, seldom more than one-fourth width of face at middle; face not descending below vibrissa (Fig. 5) .... ANGIONEURINI....12

11. Thorax with pale soft decumbent pile (often rubbed from dorsum) besides usual black setae. Preapical posterodorsal seta on hind tibia absent or hair-like .... ***Pollenia*** Robineau-Desvoidy
2 spp.; immigrant, one widespread; Shewell 1961

Thorax without pale soft pile (Fig. 21). Preapical posterodorsal seta on hind tibia present, almost as long as preapical dorsal seta (Fig. 11) .... ***Melanodexia*** Williston
8 spp.; western U.S.A.; James 1955

12. Arista plumose (Fig. 15). Apical scutellar setae long (Fig. 26) ...... ***Opsodexia*** Townsend
3 spp.; widespread

Arista short pubescent. Apical scutellar setae usually short (Fig. 27) .... ***Angioneura*** Brauer & Bergenstamm
5 spp.; widespread

13. Suprasquamal ridge with conspicuous cluster of hairs near base of scutellum (Fig. 14). Lower calypter bare above; R_5 ventrally haired beyond node. Thorax and abdomen both shining, usually metallic green .... LUCILIINI....14

Suprasquamal ridge bare or with sparse inconspicuous fine hairs near tympanic pit (Figs. 12, 13, 15). Lower calypter haired above (Fig. 12); R_5 ventrally bare beyond node. Thorax dull, pruinose; abdomen shining, usually metallic blue .... CALLIPHORINI....17

14. Subcostal sclerite with conspicuous black hairs on apical half (Fig. 17). Basicosta black ... . ***Lucilia*** Robineau-Desvoidy
1 sp., *illustris* (Meigen); widespread

Subcostal sclerite with micropubescence only (Fig. 16) 15

15. Palpus orange yellow, not darkened apically. Basicosta black or pale. Median marginal setae on tergite 3 usually absent; if present, basicosta pale .... ***Phaenicia*** Robineau-Desvoidy
8 spp.; widespread

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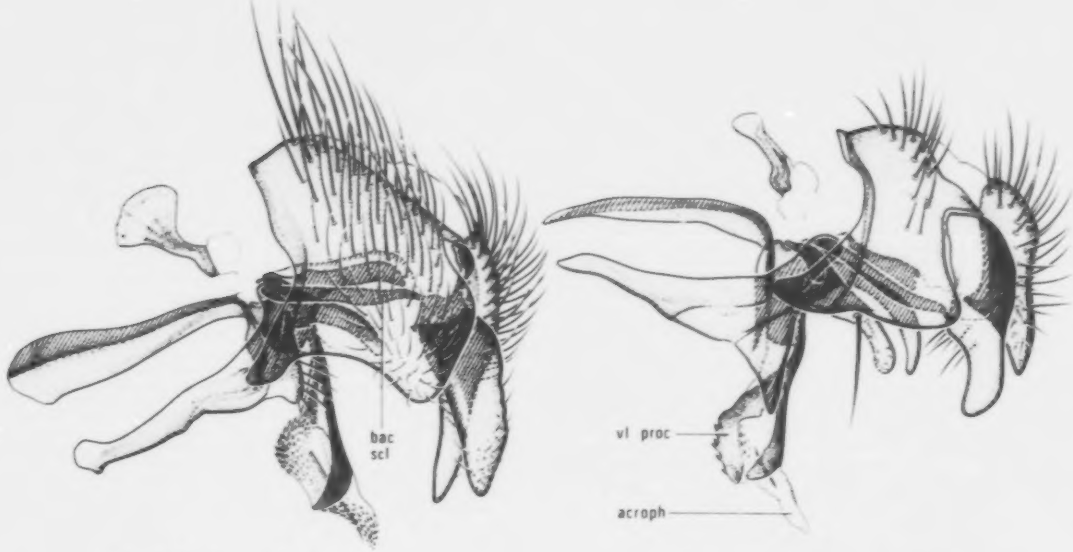
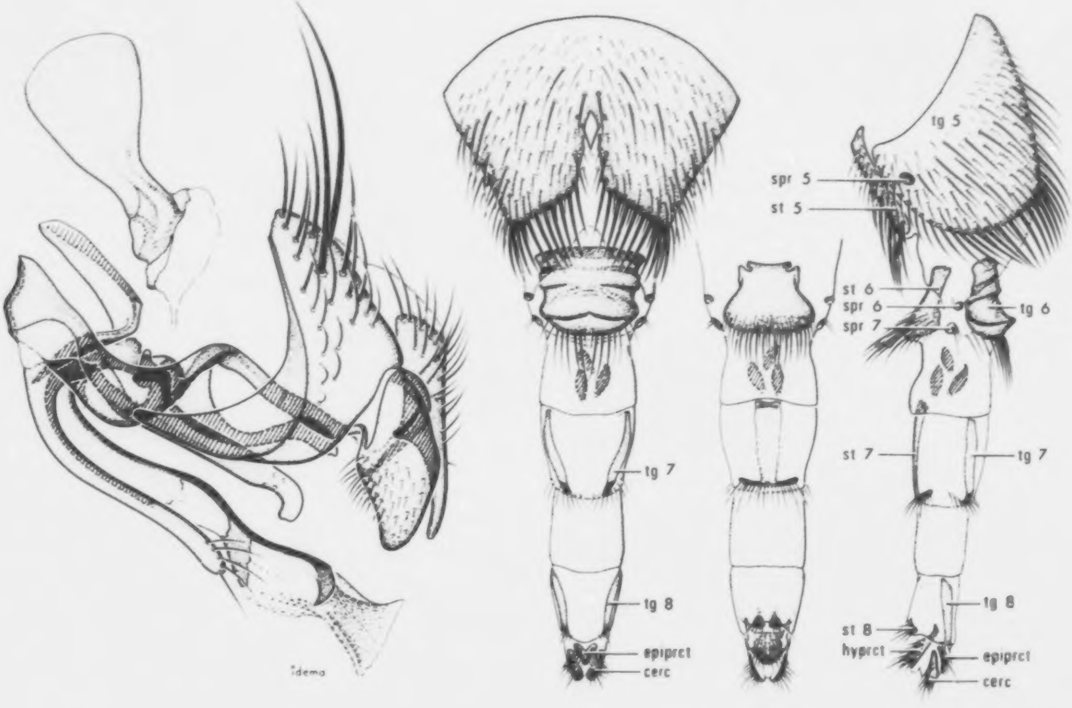
[2] Seen when wing is closed and calypter folded over.


bac scl
vl proc
acroph

30 Bellardia agilis ♂

31 Opsodexia serva ♂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32 Angioneura obscura ♂

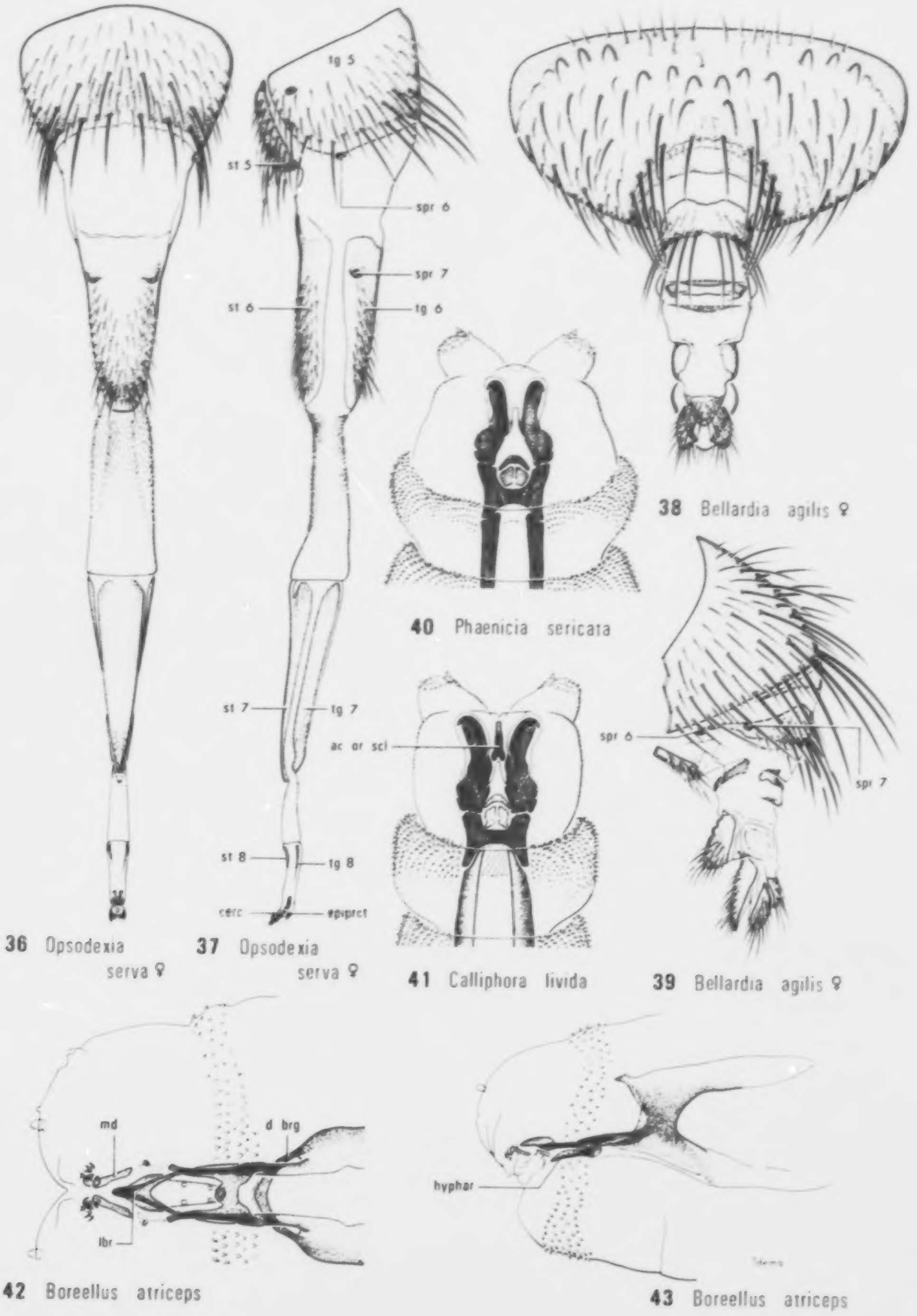
33 Acrophaga sp. ♀

34 Acrophaga sp. ♀

35 Acrophaga sp. ♀

Figs. 106.30–35. Male and female terminalia: male terminalia of (30) ***Bellardia agilis*** (Meigen), (31) ***Opsodexia serva*** (Walker), and (32) ***Angioneura obscura*** (Townsend); (33) dorsal, (34) ventral, and (35) lateral views of female terminalia of *Acrophaga* sp.

Abbreviations: acroph, acrophallus; bac scl, bacilliform sclerite; cerc, cercus; epiprct, epiproct; hyprct, hypoproct; spr, spiracle; st, sternite; tg, tergite; vl proc, ventrolateral process.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d brg
lbr
hyphar

36 Opsodexia serva ♀

37 Opsodexia serva ♀

38 Bellardia agilis ♀

39 Bellardia agilis ♀

40 Phaenicia sericata

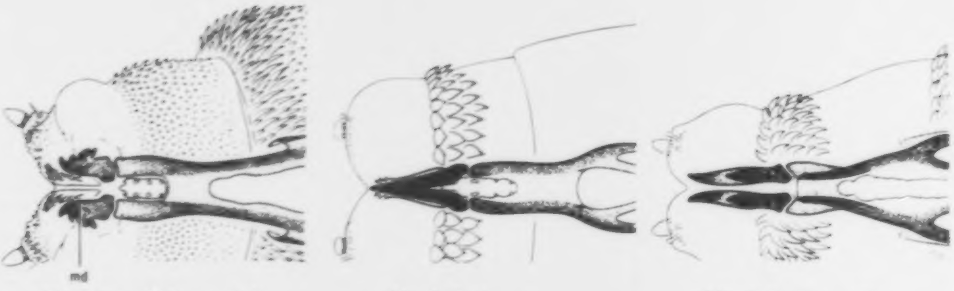
41 Calliphora livida

42 Boreellus atriceps

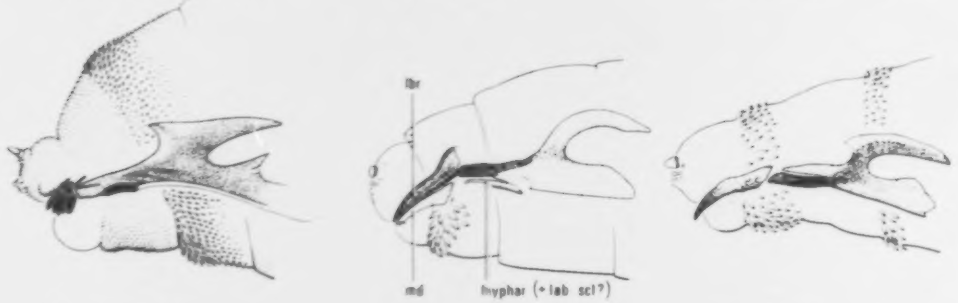
43 Boreellus atriceps

Figs. 106.36–43. Female terminalia and larvae: dorsal and lateral views of female terminalia of (36, 37) *Opsodexia serva* (Walker) and (38, 39) *Bellardia agilis* (Meigen); head of third-instar larva, ventral view, of (40) *Phaenicia sericata* (Meigen) and (41) *Calliphora livida* Hall; (42) ventral and (43) lateral views of heads of first-instar larva of *Boreellus atriceps* (Zetterstedt).

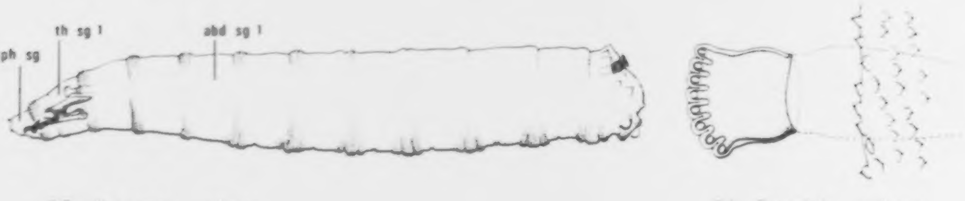
Abbreviations: ac or scl, accessory oral sclerite; cerc, cercus; d brg, dorsal bridge; epiprct, epiproct; hyphar, hypopharynx; lbr, labrum; md, mandible; spr, spiracle; st, sternite; tg, tergite.



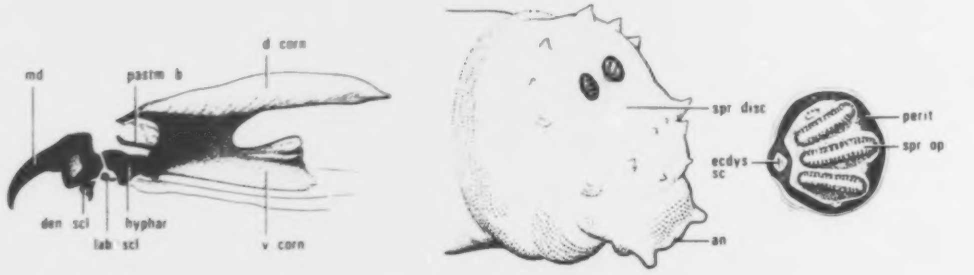
44 Protocalliphora sialia **45** Pollenia sp. **46** Bellardia agilis



47 Protocalliphora sialia **48** Pollenia sp. **49** Bellardia agilis



50 Phaenicia sericata **51** Phaenicia sericata



52 Phaenicia sericata **53** Cynomya cadaverina **54** Cynomya cadaverina

Figs. 106.44–54. Larvae: ventral and lateral views of heads of first instar of (44, 47) *Protocalliphora sialia* Shannon & Dobroscky, (45, 48) *Pollenia* sp., and (46, 49) *Bellardia agilis* (Meigen); (50) lateral view of second instar of *Phaenicia sericata* (Meigen); (51) anterior spiracle and (52) lateral view of cephalopharyngeal skeleton of third instar of *Phaenicia sericata*; (53) oblique posterior view of last segment and (54) enlarged right spiracular plate of third instar of *Cynomya cadaverina* Robineau-Desvoidy.

Abbreviations: abd sg, abdominal segment; an, anus; cph sg, cephalic segment; d corn, dorsal cornu; den scl, dental sclerite; ecdys sc, ecdysial scar; hyphar, hypopharynx; lab scl, labial sclerite; lbr, labrum; md, mandible; pastm b, parastomal bar; perit, peritreme; spr disc, spiracular disc; spr op, spiracular opening; th sg, thoracic segment; v corn, ventral cornu.

Palpus brown, more or less darkened apically. Basicosta black. Abdominal tergite 3 with one or more pairs of median marginal setae, erect in male, weaker and usually decumbent in female 16

16. Three postsutural intra-alar setae present, with anterior one weak; presutural intra-alar seta absent. Palpus light brown, slender. First antennal flagellomere large, four or five times longer than pedicel; aristal hairs decumbent, shorter than width of first flagellomere .... ***Francilia*** Shannon

1 sp., *fuscipalpis* (Zetterstedt); Arctic

Two postsutural intra-alar setae present; presutural intra-alar seta present. Palpus dark brown, clavate. First antennal flagellomere normal, about three times longer than pedicel; aristal hairs erect, longer than width of first flagellomere .... ***Bufolucilia*** Townsend

2 spp.; one widespread, one western

17. Bend of M obtuse; curvature of apical section even (Fig. 8) .... ***Bellardia*** Robineau-Desvoidy

2 spp.; Palaearctic, immigrant to eastern U.S.A.

Bend of M acute or right-angled; curvature of apical section greatest just beyond bend (Figs. 9, 10) 18

18. Presutural intra-alar seta present (Fig. 12) 19

Presutural intra-alar seta absent (Fig. 22) 21

19. Basicosta yellow. Lower calypter white .... ***Cyanus*** Hall

1 sp., *elongatus* (Hough); western

Basicosta black, or if pale, then disc of lower calypter mostly dark 20

20. Lower calypter white. Male terminalia sometimes large (Fig. 29). Female tergite 5 with median cleft posteriorly (Figs. 33, 35) .... ***Acrophaga*** Brauer & Bergenstamm

2 spp.; Arctic and alpine

Lower calypter mostly dark brown. Female tergite 5 not cleft 22

21. Lower calypter white. Pile of anterior spiracle dark brown. Abdomen shining blue or green, not noticeably pruinose except in oblique view .... ***Cynomya*** Robineau-Desvoidy

3 spp.; two boreal, one widespread

Disc of lower calypter mostly light brown; border white. Abdomen dark green, conspicuously white pruinose .... ***Aldrichina*** Townsend

1 sp., *grahami* (Aldrich); Palaearctic, immigrant to western U.S.A.

22. Genal groove and parafacial black. Usually only two strong lateral scutellar setae present besides the apical pair (Fig. 25) .... ***Acronesia*** Hall

4 spp.; widespread, boreal

Genal groove and lower parafacial chestnut brown. Usually at least three strong lateral scutellar setae present besides the apical pair (Fig. 24) 23

23. A second pair of strong divergent ocellar setae present behind upper ocelli. Facial ridge with strong short supravibrissal setae up to middle. Basicosta black. Frons of male one-fourth width of head .... ***Eucalliphora*** Townsend

1 sp., *latifrons* (Hough); western, rare in east

Only one pair of strong ocellar setae present. Facial ridge with only fine supravibrissal hairs above. If ridge more setose, then basicosta yellow or male frons much less than one-fourth width of head .... ***Calliphora*** Robineau-Desvoidy

6 spp.; widespread

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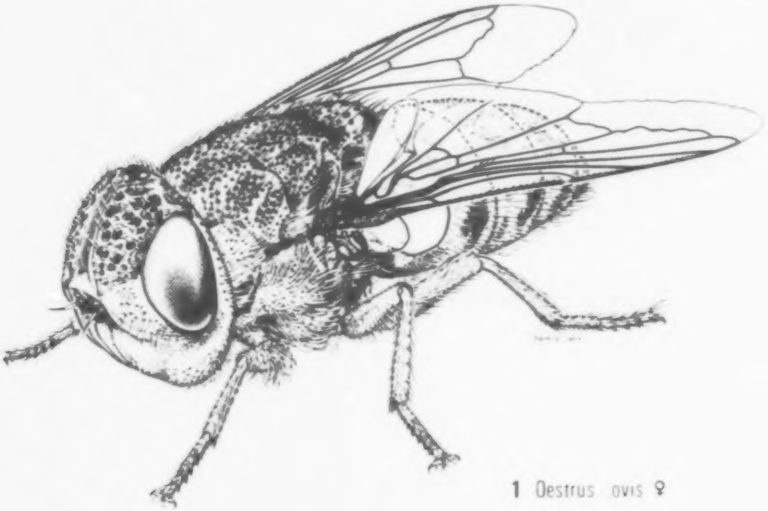
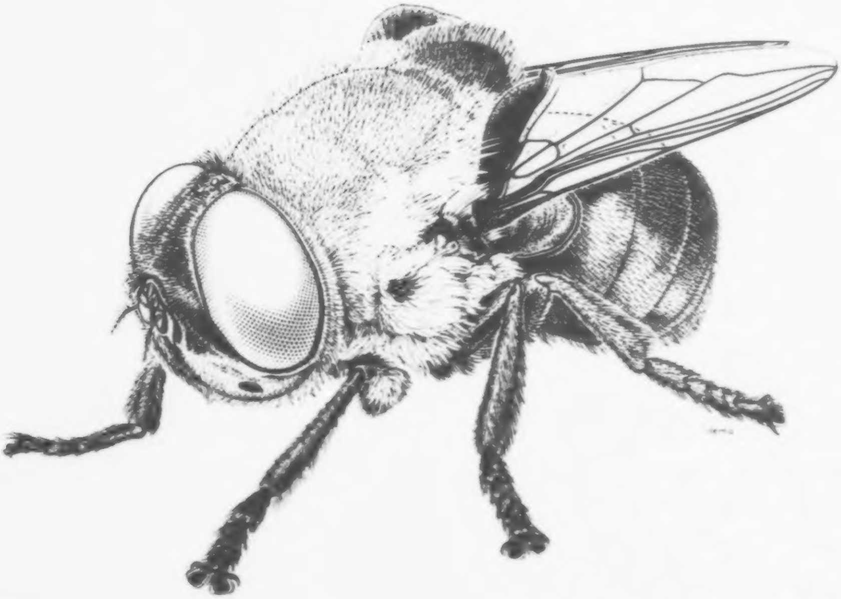
OESTRIDAE

107

D. M. Wood



1 Oestrus ovis ♀



2 Cuterebra emasculator ♂

Figs. 107.1–2. (1) Female of *Oestrus ovis* Linnaeus; (2) male of *Cuterebra emasculator* Fitch.

Medium-sized to very large heavy-bodied flies (Figs. 1, 2), 9-25 mm long, with small, compact, or atrophied mouthparts, small antennae, and pilose bristleless bodies. Some species resemble honey, carpenter, or bumble bees.

Adult. Head: usually broad, flattened front to back, subcircular in anterior view (Figs. 3, 4). Eye rather small. Gena and genal groove correspondingly extensive. Frontal vitta smooth and pilose, usually obscurely differentiated; male frons seldom strongly narrowed. Antenna small and compact, deeply sunk into antennal pit; first flagellomere usually globular, fitting into cup-like pedicel; arista slender and bare with bulbous base, or in *Cuterebra* Clark plumose and without swollen base. Face flat, either broad and shield-shaped or abruptly constricted below antennae, bare or pilose; facial ridge flat, pilose. Subcranial cavity either small and hastate or pyriform with slit-like anterior portion, or small and oval, or virtually absent. Proboscis small but functional, vestigial, or absent; palpus small and haired, or in the form of a minute sessile hairless knob, or absent.

Thorax: pilose (Fig. 1) to densely long-haired (Fig. 2), rarely with weak bristles; scutum and scutellum (Figs. 9, 10) clothed with long dense erect pile or short and recumbent pile; meron with a patch of hair posteriorly, or rarely with a row of fine bristles, or bare; remainder of pleuron extensively pilose. Subscutellum (Figs. 9, 10) usually a narrow transverse bar, but if better developed, then upper half narrower and less convex than lower half, rarely in some exotic genera nearly as convex as in the Tachinidae. Legs short, stout, robust, hairy; femora and tibiae often with short weak bristles; apices of tibiae and tarsal segments usually with short spine-like bristles. Vein M of wing variable, straight or slightly curved posteriorly to end in wing margin well behind wing tip (Fig. 5), or curving evenly forward to end in C just behind tip of R_{4+5} (Figs. 7, 8), or strongly angled with prominent stump vein beyond crossvein dm-cu (Fig. 7); crossvein dm-cu in usual position (Figs. 6-8), or strongly retracted almost to level of crossvein r-m (Fig. 5), or absent.

Abdomen: globose (Fig. 2) to conical (Fig. 1), with shiny integument and long colored pile, or partly or entirely pruinose. Male sternite 5 small, simple, without deep apical cleft; male terminalia (Fig. 11) small, strongly retracted, and carried rather far forward on underside of abdomen; syntergosternite 6 + 7 + 8 relatively large, nearly as large as tergite 5 in some genera; surstylus usually rounded apically, short, stout, rather widely separated, and usually longer than cerci; aedeagus short, with scarcely differentiated distiphallus; epiphallus usually present. Ovipositor (Figs. 12-14) short and simple, or elongate and fully retracted, or extended and carried folded beneath abdomen; sternite 8 partially or fully divided longitudinally.

Egg. Transparent and delicate in viviparous forms, or pale yellowish brown, with tough leathery chorion and well-differentiated operculum in oviparous genera (Figs. 15-17). Adhesive ventral surface flattened in those genera ovipositing on objects other than host (Fig. 15), or variously modified as a holdfast for attachment to a hair (Figs. 16, 17).

Larva. First instar white, usually with one or two bands of spines on each segment; both mandibles equally well-developed; posterior spiracle minute or absent. Second instar usually whitish, variously spined; posterior spiracle either with two cross-barred slits or with a circular sieve plate having fewer than 100 pores. Third instar at maturity (Fig. 18) large, stout, and heavily spined or encrusted with platelets; mandible usually strong, curved; posterior spiracle with three curved cross-barred slits (Fig. 19), three groups of numerous closely intertwined slit-like openings (Fig. 20), or a sieve plate with many more than 100 pores enclosing prominent circular scar of second instar spiracle (Fig. 21).

Biology and behavior. All Oestridae, as larvae, are obligate parasites of mammals. Most species show a high level of host specificity (Baird 1972; Catts 1965, 1982). Immature larvae removed from their hosts invariably die and have apparently not been successfully reared *in vitro*. In contrast, some parasitic calliphorids and sarcophagids have been reared on artificial media and, if deprived of food, produce smaller adults. In contrast, wild-caught adults of a given species of oestrid are quite uniform in size.

Adult oestrids are distinct from other calyptrates by having minute or atrophied mouthparts, and apparently none has been observed taking sugar or protein as do most other calyptrates, relying instead on stored fat. Among the Oestridae, *Cephenemyia* Latreille can imbibe fluids by pressing the ventral surface of the head to a moist substrate (Catts and Garcia 1963) and *Cuterebra* also seems capable of doing so (Bennett 1955), but the mouthparts of several genera in each of the oestrid subfamilies show varying degrees of atrophy to the point where external structures are quite unrecognizable (e.g. *Oestrus* Linnaeus, *Hypoderma* Latreille, *Gasterophilus* Leach). Adults of most species are rare in collections; most are known from few adult specimens, and a few species are known only from larvae.

Males of some species assemble for mating purposes at topographic features such as on hilltops (Catts 1967, 1979) or near bodies of water, where they are rather easily caught. Estimates of their flight speed in excess of the speed of sound (Townsend 1926, cited by Townsend 1942) brought the family wide publicity, but these reports have since been thoroughly discredited as gross exaggeration.

Adult females are difficult to obtain, but can be reared from mature larvae. A few have been captured in Malaise traps baited with carbon dioxide (Anderson and Olkowski 1968) or occasionally have been taken near their hosts (e.g. *Gasterophilus*). The female emerges with its complement of eggs fully developed in the ovarioles. After fertilization, the eggs are laid on some part of the host, usually on the hair, or on objects with which the host is likely to come into contact. Eggs require a few days to embryonate. A noteworthy exception is the tribe Oestrini, in which the eggs are embryonated *in utero* (Catts 1964) and active maggots are deposited in a drop of fluid into the nostrils of the host (reviewed by Golini *et al.* 1968 and by Anderson 1975). Second- and third-instar larvae are relatively sedentary, occupying a specific niche in the body of the host: some in the gut wall and others in the respiratory passages or within pockets in the skin where they have access to air through a small perforation to the exterior. Upon reaching maturity all species abandon the host and enter the soil to pupate. Species of *Cuterebra* overwinter as puparia in the ground; others overwinter as larvae in the host.

Many authors have observed that horses, cattle, sheep, and reindeer, when under attack by certain oestrids, become nervous or panic-stricken, and may even stampede, a reaction they do not show to other pestiferous flies. These reactions differ among different species of host.

Classification and distribution. In the 19th century, the calyptrate Diptera whose larvae were obligate internal mammalian parasites were generally placed together as one family, the Oestridae (Brauer 1863, Brauer and Bergenstamm 1889). As muscoid family characters were elucidated, however, the various oestrid genera were dispersed. *Gasterophilus* was assigned to the Muscidae or even to the acalyptrates (Séguy 1928) because its members possessed small calypteres and a straight vein M. Other genera were relegated to the Calliphoridae or the Tachinidae depending on the size of the subscutellum (Emden 1944, Zumpt 1957, reviewed by Papavero 1977). Hardly any two authors have agreed in their treatment of the genera, whose origins and phylogeny are still uncertain. Phylogenetic studies have led some recent workers to again regard the Oestridae either as a single family (Hennig 1952; Herting 1955, 1957) or as three families that are probably more closely related to one another than to any other (Hennig 1973), hence forming a monophyletic group. No one has yet shown convincingly that the group is not monophyletic; if one examines the similarities among the genera rather than the differences, several features that are common to all genera and that appear to be shared derived characters (synapomorphies) set them aside from other calyptrates. Consequently the group is treated here as a single monophyletic family.

Four subfamilies, Cuterebrinae, Gasterophilinae, Hypodermatinae, and Oestrinae, are here recognized, corresponding closely to those families or subfamilies of the same name of other authors. The Hypodermatinae and the Oestrinae share, as an apomorphic character state, the sieveplate-like posterior larval spiracle. This is evidently a unique character state in the Oestroidea, and perhaps also in the Calyptratae, and is evidence that the two taxa form a monophyletic group. They have often been united as a single family, Oestridae (e.g. Chillcott 1965), and are regarded here as sister taxa. Unfortunately the phylogenetic relationships between Hypodermatinae and Oestrinae and the remaining two subfamilies are not as readily apparent and have not yet been worked out. Further details about each subfamily are given below.

The family is best represented in Africa and central Asia. The African elephant has the greatest diversity of parasites, supporting five species, each placed by Zumpt (1965) in a different genus (and in four genera in Table 1). Many of the African and central Asian ungulates (both Artiodactyla and Perissodactyla) also are afflicted. Members of the Hypodermatinae of central Asia, in contrast, parasitize rodents and lagomorphs as well as Artiodactyla. The North American oestrid fauna is much poorer; aside from a few introduced species of *Gasterophilus*, *Hypoderma*, and *Oestrus* on domestic animals imported from Europe, only the genus *Cuterebra* parasitizing rodents and lagomorphs, several species of *Cephenemyia* which live in cervids in mountainous and northern regions, and a Holarctic species, *Hypoderma tarandi* (Linnaeus), which afflicts caribou, are known. Humans are only infected accidentally, in which case the larvae do not mature although they may cause considerable discomfort (James 1947). A few fossil larvae, alleged to be oestrid, are discussed by Townsend (1942).

Cuterebrinae: This subfamily is restricted to the New World (unless either or both of the elephant skin parasites, discussed below, are shown to belong to this subfamily). Nearctic members of Cuterebrinae all belong to the genus *Cuterebra* and are parasites of small rodents and lagomorphs, especially mice, squirrels, pack rats, and rabbits. Infection has been recorded in a wide variety of hosts, but most species of Nearctic *Cuterebra* develop normally in only a single species, or a group of closely related species, of native North American mammals. However, non-native ones (such as the European hare), which presumably have not developed resistance, may also serve as suitable hosts (Catts 1965). Eggs are not laid on the host, but in places frequented by a suitable host, and after several days of embryony they hatch quickly in response to sudden warming in the presence of a potential host. In seconds the first instar pushes off the loosely attached operculum of the rigid eggshell (Fig. 15) and extends its mandibles, ready to grasp a hair. Infection apparently takes place through any body orifice, but regardless of the point of entry, first instar larvae (of *Cuterebra grisea* Coquillett at least) migrate to deep nasal or tracheal sites where they remain for some time before emigrating to subcutaneous tissues (Hunter and Webster 1973). The remaining larval stages are passed in the warble, a pouch (furuncle) formed by the host in the connective tissue within the skin (Bennett 1955); the posterior spiracles of the larva communicate with the air through a small opening. The position of the warble on the host is rather constant; those parasitizing rabbits tend to develop on the neck, while those in mice and chipmunks are usually on the belly. The developing larva appears to have little gross effect on its host, although changes in weights of specific internal organs have been noted (Catts 1982). When mature the larva backs out through the air hole, especially when the host is active, apparently without disturbing the host. Pupation takes place in the ground. The winter is passed in the puparium. Adults appear in early summer in northern regions; at lower latitudes some species may have more than one generation, with adults appearing also in late summer. They are rarely encountered except at male aggregation sites (Catts 1982, Schiffer 1983).

Third-instar larvae of *Cuterebra* are apparently unique among oestrids in being almost entirely encrusted with small flattened plate-like spines, which may act as a suit of armor, or help to prevent desiccation. These plate-like spines are regarded here as a synapomorphy of the genus *Cuterebra*.

Earlier instars have thorn-like spines encircling the segments, as do other oestrids. Members of the subfamily (*Cuterebra* and *Dermatobia* Brauer at least) also share a unique feature: the anterior felt chamber is evaginated through the anterior spiracle when the puparium is formed. The anterior spiracle is a simple, unsclerotized, slit-like opening (unlike the typical sclerotized, fan-shaped or finger-like protuberance of other Muscomorpha) not visible in the mature larva. Each evaginated felt chamber resembles a small, orange yellow, velvet pompom, which has previously been incorrectly called the anterior spiracle. At pupation, the posterior spiracles are withdrawn inwardly and are almost closed off by the antepenultimate segment.

The subfamily Cuterebrinae is generally considered exclusively American. Although only members of the genus *Cuterebra* are known from the Nearctic region, several other genera of Cuterebrinae occur in the Neotropical region (Table 1), where the larvae form cutaneous warbles in rodents, lagomorphs, monkeys, domestic livestock, and humans. The unusual Neotropical cuterebrid, *Dermatobia hominis* Linnaeus Jr., attacks many different hosts, including birds and various mammals, including humans. The female first catches a free-living, blood-sucking fly, such as a mosquito or stable fly, on which she lays her eggs. This carrier then transmits the eggs to the host, where the warmth of its body triggers hatching. First-instar larvae do not migrate in the tissues of the host, as do most other oestrids, including *Cuterebra*, but develop to maturity where they enter, as do parasitic calliphorids. Larval development at the site of infection is regarded here as the plesiomorphic condition. Unlike third instars of *Cuterebra*, those of *Dermatobia* have only a single encircling ring of thorn-like spines, presumably also the plesiomorphic condition.

Two subdermal parasites of the African elephant, *Ruttenia loxodontis* Rodhain and *Neocuterebra squamosa* Grünberg, of uncertain systematic position (they were tentatively placed in Gasterophilidae by Zumpt (1965)), have larvae that appear to possess plate-like spines similar to, and perhaps homologous to, those of *Cuterebra* larvae. Unfortunately, their life-cycles are unknown, so it is not known whether first-instar larvae develop where the eggs are deposited (as in Calliphoridae), or migrate from the point of entry to their final site in the skin, as do larvae of Hypodermatinae and *Cuterebra*. The possible relationship between these two African genera and New World Cuterebrinae has not been investigated.

Gasterophilinae: No members of this subfamily are endemic to the Americas, but four species of *Gasterophilus* were introduced with horses in the earliest days of settlement, and three are now widespread on both continents. Males wait for females while hovering about the host or at hilltop aggregation sites (Catts 1979). Eggs of a single member of the group, *G. pecorum* (Fabricius), are laid on the tips of grass blades (Zumpt 1965) (suggestive of the oviposition behavior of Cuterebrinae); those of all other species are cemented onto the hairs of the lips, chin, cheeks, or forelegs of the host, the position depending on the species of *Gasterophilus* (Hadwen and Cameron 1918). Larvae hatch and burrow spontaneously, or hatch when licked, after which they attach themselves to the tongue; all species ultimately spend the first instar in the mouth tissue (Cogley *et al.* 1982), where they can cause considerable destruction of the gums. Second instars of all species leave the mouth tissue and descend to the stomach, duodenum, or rectum, where they complete their development. Large numbers of maturing larvae may puncture the stomach wall, or obstruct the gut, sometimes with fatal results. Mature larvae of *Gasterophilus* and *Gyrostigma* finally leave the host through the anus and pupate on the ground, usually beneath the fecal pile, whereas those of *Cobboldia* apparently escape from the mouth.

African and Asian oestrids include several species of *Gasterophilus* in horses and zebras, three species of *Gyrostigma* Brauer in rhinoceroses, and three species of *Cobboldia* Brauer (placed by some authors, including Zumpt (1965) in three scarcely different genera) in elephants. Adults of *Gasterophilus* and *Gyrostigma* have atrophied mouthparts, a straight vein M, and small calypteres, but those of *Cobboldia* appear to have complete, though minute, mouthparts, normal calypteres, and normal wing venation. Yet, based on larval structure and habits, all three genera appear to form a monophyletic taxon. The parallel elongate openings of the larval posterior spiracle are peculiar to these genera and are presumably also a synapomorphy.

Hypodermatinae: This subfamily is represented in North America by only three species, *Hypoderma tarandi*, a Holarctic parasite of caribou, and *H. bovis* (Linnaeus) and *H. lineatum* (Villers), both introduced from Europe on cattle. By force of habit, *H. tarandi* usually has been placed in a separate genus, *Oedemagena* Latreille, because of the presence of minute palpi. However, the mouthparts, including palpi, are atrophied to such various degrees in each line of oestrids, and even among the species of *Gasterophilus*, that this character seems subject to frequent parallelism and is thus of scant generic value. In this context, it should be kept in mind that generic names have also been proposed for each of the common species of *Gasterophilus* and for each species of *Cobboldia* as well, yet these names are generally ignored. Use of them emphasizes differences rather than shared apomorphies.

Males of *Hypoderma* do not seek high points, but instead, wait for females alongside small streams (Catts *et al.* 1965). Eggs are attached to hairs of the host, usually on the legs and flanks, by a petiolate holdfast arising from the posterior end of the egg (Fig. 16). Newly hatched larvae burrow into the skin, then migrate to the esophagus (*H. lineatum*) or spinal canal (*H. bovis*) before reaching the skin of the back. Their advance is facilitated by enzymatic dissolution of the tissue, the enzymes presumably secreted from their salivary glands (Wolfe 1959). Large numbers of larvae cause skin lesions on entering the host, which can be fatal to young caribou (Hadwen 1926). Second and third instars of the Hypodermatinae inhabit cutaneous open cysts, or warbles, as do the cuterebrines, but unlike the latter, larvae have vestigial mandibles and their integument lacks the heavy armament of plates. Anterior spiracles are minute or rudimentary and not visible on the puparium. The posterior spiracles are large and circular or C-shaped, with numerous minute pores over the entire plate. The posterior spiracle of the third

Table 1. Host relationships and distribution of world Oestridae[1]

Subfamily and genus	Number of species	Hosts	Larval site in host	Geographic range
CUTEREBRINAE				
Alouattamyia	1	howler monkeys	skin	South America
Andinocuterebra	1	?	?	South America
Cuterebra	60+	rodents, lagomorphs	skin	New World
Dermatobia	1	many mammal species	skin	South America
Pseudogametes	2	?	?	South America
Rogenhofera	6	?	?	South America
CUTEREBRINAE (?)				
Neocuterebra	1	African elephant	skin	West Africa
Ruttenia	1	African elephant	skin	West Africa
GASTEROPHILINAE				
Gasterophilus	9	horses, zebras	gut	Eurasia, Africa 3 spp., secondarily cosmopolitan
Gyrostigma	3	rhinos	gut	Africa, Oriental
Cobboldia	3	elephants	gut	Africa, Oriental
HYPODERMATINAE				
Hypoderma	5	Cervidae, cattle	skin	Eurasia, 1 sp. Holarctic, 2 spp. secondarily cosmopolitan
Oestroderma	1	pikas	skin	Central Asia
Oestromyia	5	mice, marmots, pikas	skin	Eurasia
Pallasiomyia	1	saiga antelope	skin	Central Asia
Pavlovskiata	1	goitered antelope	skin	Central Asia
Portschinskia	7	mice, pikas	skin	Eurasia
Przhevalskiana	6	gazelles, goats	skin	Central Asia
Strobiloestrus	3	*Kobus* spp.	skin	Africa
OESTRINAE				
Cephalopina	1	camels	nasal passages	Asia
Cephenemyia	8	Cervidae[2]	nasal passages	Holarctic
Gedoelstia	2	antelopes[3]	nasal passages	Africa
Kirkioestrus	2	antelopes	nasal passages	Africa
Oestrus	6	antelopes, sheep, goats	nasal passages	Eurasia, Africa
Pharyngobolus	1	African elephant	trachea	Africa
Pharyngomyia	2	Cervidae	nasal passages	Eurasia
Rhinoestrus	11	horses, zebras, pigs giraffe, hippopotamus springbuck, sheep	nasal passages	Eurasia, Africa
Tracheomyia	1	kangaroos	trachea	Australia

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[1] Treatment of Cuterebrinae follows Chillcott (1965) and Guimaraes (1967); that of the other subfamilies (including *Ruttenia* and *Neocuterebra*) is from Bennett and Sabrosky (1962) for *Cephenemyia* and Zumpt (1965) for the rest.

[2] Members of the Cervidae parasitized are deer (*Cervus*, *Odocoileus*), wapiti (*Cervus*), caribou (*Rangifer*), and moose (*Alces*).

[3] Included here are several bovine genera belonging to the tribe Alcelaphini, viz. wildebeest (*Connachaetes* spp.), hartebeest (*Alcelaphus* spp.), and members of the genus *Damaliscus*, and the tribe Hippotragini, e.g. *Hippotragus* and *Oryx*.

instar shows within it a prominent circular scar of the second instar spiracle. Pores are arranged randomly as in Oestrinae, without evidence of a triad as in Cuterebrinae or Gasterophilinae; this character is probably derived. Overwintering occurs in the host, and the mature larva escapes the cyst through an opening in the skin during the spring to pupate in the ground. The puparium is concave dorsally; only the upper valve is detached at eclosion.

The center of diversity of the Hypodermatinae is in Central Asia, with a few species extending into Europe and Africa (Zumpt 1965). Hosts are ungulates, especially deer, antelopes, and goats; rodents such as marmots and mice; and pikas (Lagomorpha).

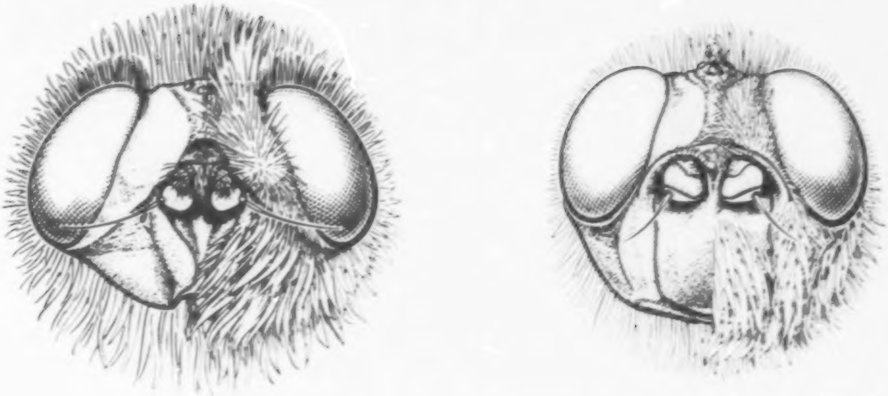
Oestrinae: Members of this subfamily are readily distinguished from other oestrids because their larvae inhabit respiratory passages of their hosts, rather than the gut or skin. The species also share a distinctive synapomorphy unknown in other calyptrates: eggs are retained in an elaborately tracheated bilobate uterus until ready to hatch (Catts 1964). The uterus is a diverticulum of the common oviduct, as in the Sarcophagidae, not the oviduct itself, as in the Tachinidae. Females consequently larviposit rather than oviposit, and first-instar larvae are forcibly expelled within droplets of fluid in the vicinity of the nostrils of the host. Until recently first instars were assumed to enter by the nostrils and crawl up the nasal passages to the sinuses or to various other nasopharyngeal recesses. However, critical observations have now shown that, for two species of *Cephenemyia* at least, first instars crawl down toward the upper lip, enter the mouth, and reach the throat via the hard palate (Cogley and Anderson 1981). Developing larvae feed on blood and secretions, and when numerous they can cause enlargement and damage to the cavities in which they are feeding (Bennett 1962). The larvae overwinter in the host, and when mature crawl back out through the nostrils to the accompaniment of much snorting and sneezing on the part of the host. Anterior spiracles are present, though small, in larvae of *Cephenemyia* but are withdrawn when the puparium is formed; they appear to be lacking in *Oestrus*. The puparium of *Cephenemyia* has both upper and lower valves (presumably the plesiomorphic condition); that of *Oestrus*, like that of *Hypoderma*, has only the upper valve, the lower one remaining fused to the remainder of the puparium.

In North America, *Oestrus ovis* Linnaeus was introduced with domestic sheep; the remaining Oestrinae, all belonging to *Cephenemyia*, inhabit all the native cervids, namely caribou, deer, wapiti, and moose (Bennett and Sabrosky 1962).

The center of oestrine diversity is in Africa, where a variety of Artiodactyla are afflicted, as well as elephants, rhinos, and horses (Zumpt 1965). The species in the African elephant, *Pharyngobolus africanus* Brauer, apparently occupies the esophagus as well as the throat; larvae leave the host via the trunk. Oestrinae are also widespread in the Palaearctic region, infecting camels, horses, and goats. A single species, *Tracheomyia macropi* (Froggatt), occurs in Australia in the tracheae of kangaroos.

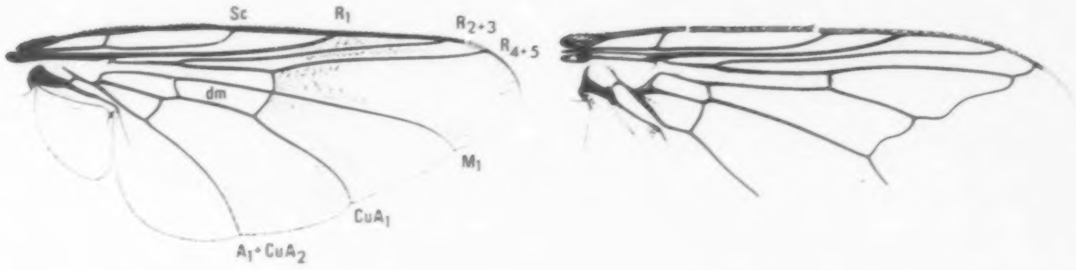
The presence of an oestrid in such an unusual host and region prompted Papavero (1977) to invoke continental drift as an explanation. He presented a cladogram (his fig. 53) hypothesizing the phylogenetic relationship between four taxa of Oestridae (Oestrinae *sensu* this chapter), namely the Cephenemyiinae (with two genera, *Cephenemyia* and *Pharyngomyia* Schiner), the Pharyngobolinae (*Pharyngobolus* Brauer only), the Tracheomyiinae (*Tracheomyia* Townsend only), and the Oestrinae (all remaining genera). The last two subfamilies were shown as sister taxa, while their sister group was the Pharyngobolinae. The Cephenemyiinae formed the ancestral lineage of the other three subfamilies. Paravero postulated that this assemblage originated in Pangaea during the Jurassic, at least 150 million years ago, when fossil evidence suggests that mammals were quite small. Evidence that any members of the Schizophora were present that early is also lacking. From this doubtful origin he hypothesized the subsequent isolation of the two basic lineages, the Cephenemyiinae in Laurasia and the Pharyngobolinae + Oestrinae + Tracheomyiinae in Gondwanaland. The ancestor of the latter three taxa was then postulated to hve been the precursor of the Pharyngobolinae in Africa, the Oestrinae in Africa and Asia, and the Tracheomyiinae in Australia. Such an early origin of oestrids required postulation of suitable hosts, of which, for mammals at least, there are no known fossil records. Papavero's entire theory rests on the soundness of his single cladogram, which was not documented by any shared derived character states. Any rearrangement of that cladogram could profoundly influence the zoogeographic conclusions.

During the Palaeocene, 55–60 million years ago, the order Condylarthra, a group of subungulates with some moderately large members, occupied various continents (Romer 1966) and may have been virtually world wide. Two orders of early ungulates, Notoungulata and Litopterna, developed from the Condylarthra during the Palaeocene, and, in association with marsupials, flourished in South America during the Eocene. Some of these ungulates were very large, up to 3 m in length, sufficiently large to serve as hosts for oestrids. Although having been separated from Africa for at least 50 million years, South America in the Palaeocene was still in contact with North America to the north and with Antarctica and Australia in the south (Howarth 1981). Australia and Antarctica remained together as a single continent for several million years longer. South America must have been joined to it, either by a direct connection, or by an island chain, presumably the present Scotia Arc, and it has been suggested that marsupials, which are believed to have originated in North America and flourished in South America during the Palaeocene, may have gained entry from the Americas to Australia via Antarctica at that time. It is possible that the ancestor of *Tracheomyia* may have accompanied some of the largest marsupials into Australia at the same time. The early ungulates apparently did not pass from South America to Australia, for their fossils are not known outside of South America. The question of how the ancestor of *Tracheomyia* arrived in Australia remains unsolved.



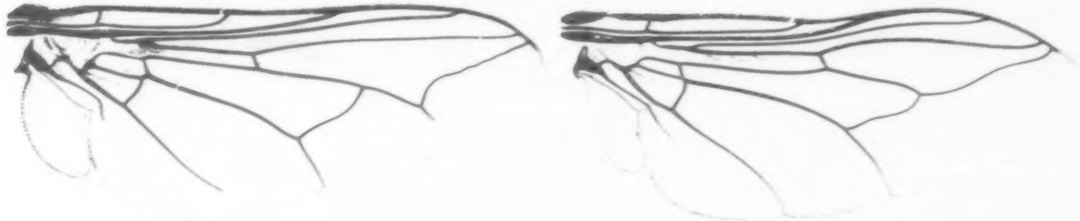
3 Cephenemyia trompe ♀

4 Hypoderma bovis ♂



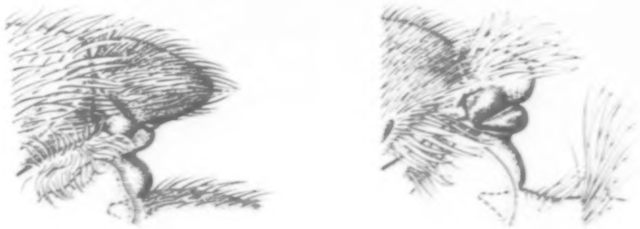
5 Gasterophilus intestinalis ♂

6 Oestrus ovis ♂



7 Cephenemyia trompe ♀

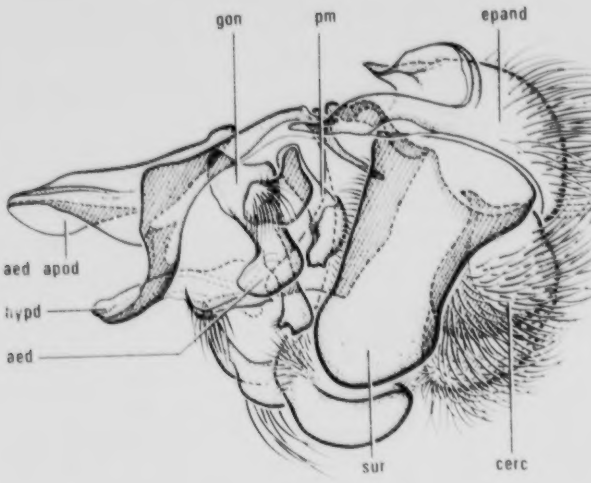
8 Hypoderma bovis ♂



9 Cuterebra grisea ♀

10 Hypoderma bovis ♀

Figs. 107.3–10. Heads, wings, and thoraces: frontal views of heads of (3) *Cephenemyia trompe* (Modeer) and (4) *Hypoderma bovis* (Linnaeus); wings of (5) *Gasterophilus intestinalis* (De Geer), (6) *Oestrus ovis* Linnaeus, (7) *Cephenemyia trompe*, and (8) *Hypoderma bovis*; left lateral views of posterior portion of thoraces of (9) *Cuterebra grisea* Coquillett and (10) *Hypoderma bovis*.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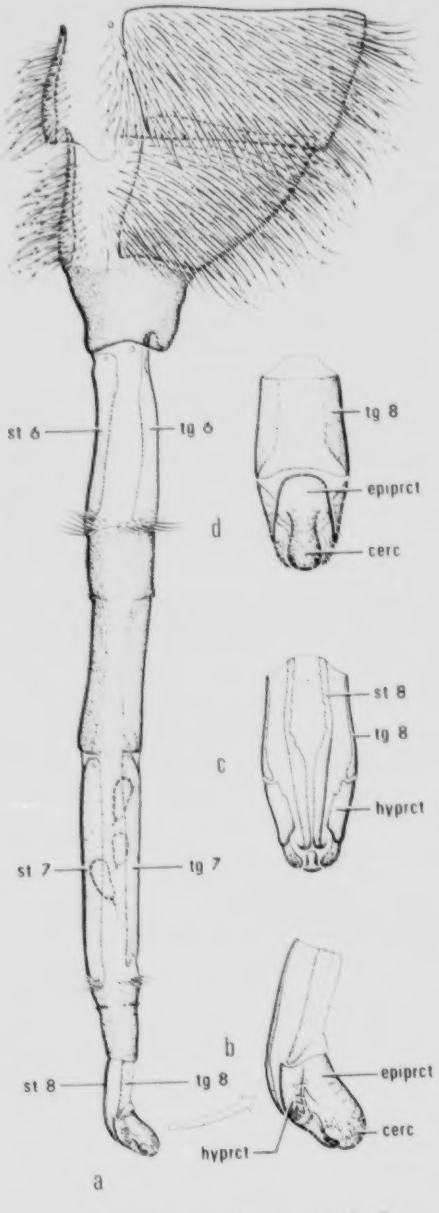
11 Gasterophilus intestinalis ♂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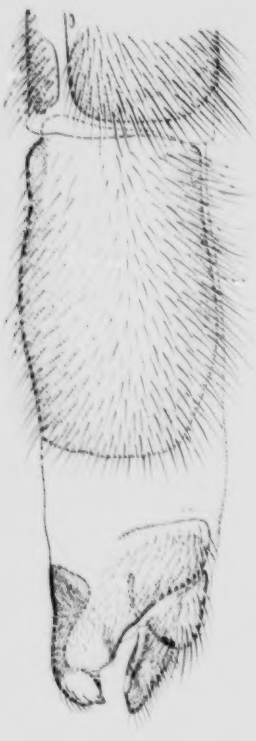
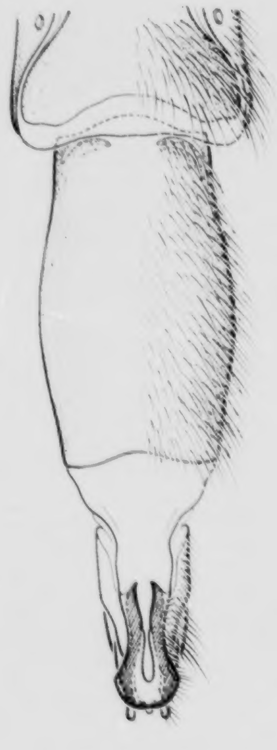


12 Gasterophilus intestinalis ♀

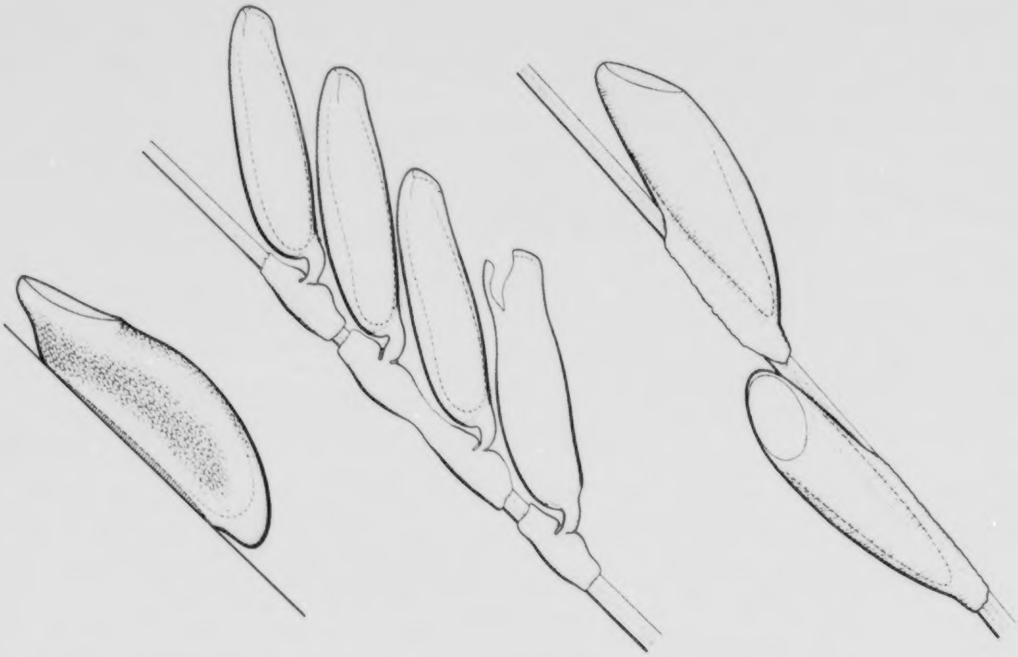


13 Gasterophilus intestinalis ♀

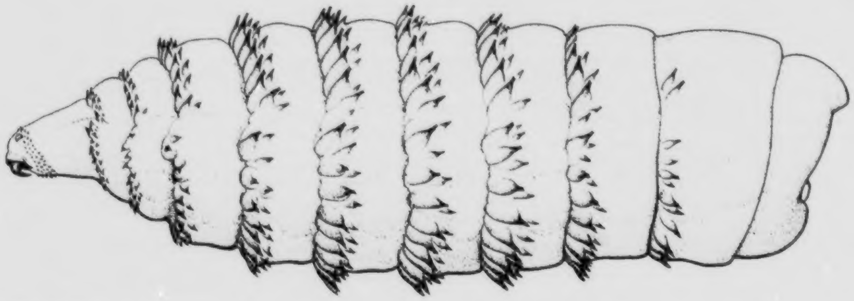
14 Hypoderma bovis ♀

Figs. 107.11–14. Terminalia: (11) ventrolateral view of male terminalia of *Gasterophilus intestinalis* (De Geer); (12) lateral and (13) ventral views of female terminalia of *Gasterophilus intestinalis*; (14*a*) lateral view of female terminalia of *Hypoderma bovis* (Linnaeus); (14*b*) apex of same, enlarged; (14*c*) ventral view of apex of same; (14*d*) dorsal view of apex of same.

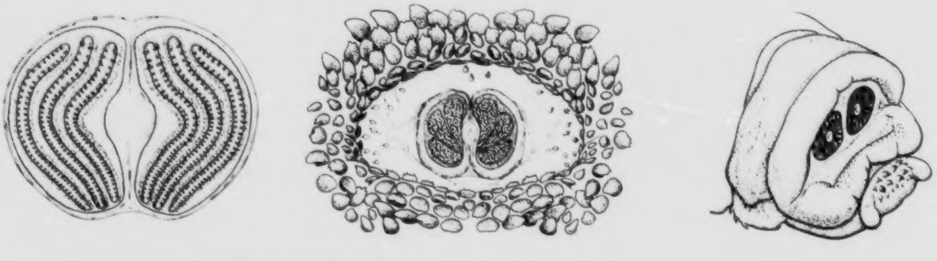
Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; st, sternite; sur, surstylus; tg, tergite.



15 Cuterebra emasculator **16** Hypoderma lineatum **17** Gasterophilus intestinalis



18 Gastrophilus intestinalis



19 Gastrophilus intestinalis **20** Cuterebra emasculator **21** Oestrus ovis

Figs. 107.15–21. Eggs and larvae: eggs of (15) *Cuterebra emasculator* Fitch, (16) *Hypoderma lineatum* (Villers), and (17) *Gasterophilus intestinalis* (De Geer); (18) lateral view of larva of *Gasterophilus intestinalis*; posterior view of posterior spiracles of larva of (19) *Gasterophilus intestinalis* and (20) *Cuterebra emasculator*; (21) oblique view of posterior end of larva of *Oestrus ovis* Linnaeus.

If species of Oestrinae occupied the New World during the early Tertiary, what ultimately became of their members? No species of *Oestrus*, *Rhinoestrus* Brauer, *Pharyngomyia*, or *Cephalopina* Strand are native to North or South America, even though their present hosts (sheep, deer, and camels) occur today in both New and Old worlds. Similarly, no representatives of the diverse Central Asian fauna of Hypodermatinae (Table 1) occur in the New World, except as introductions, even though some of their hosts (e.g. mice, marmots, and pikas) are found today in both New and Old worlds, and also live today in Beringia. Except for the two oestrids in caribou, *Cephenemyia trompe* and *Hypoderma tarandi*, only the genus *Cephenemyia* has species in both Palaearctic and Nearctic regions, yet none has penetrated the tropics, whereas their hosts, deer (Cervidae), occur widely in South America and the Oriental region.

The nature of the connections between North America and Eurasia during the Tertiary, the pre-Pleistocene extinctions of the native fauna of South America in the Pliocene following the arrival of mammal species from the north, and the post-Pleistocene extinctions in North America, following the advent of humans, must all have had a marked effect on New World oestrids. The North Atlantic "bridge" in the early Tertiary, and later, the Beringian land "bridge", probably acted as filters, less restrictive to warm-blooded mammals living there than to their oestrid parasites. At numerous intervals in the Pleistocene, and possibly to a lesser extent in the late Tertiary, the Beringian land "bridge" was more a barrier than a filter, because periods of cold and dryness during full glacial periods must have adversely affected oestrid survival. In such instances, it probably operated as a two-step barrier, i.e. either a continental ice sheet separated Beringia from the rest of North America for several 1000-year periods during full-glacial periods, or the open water of Bering Strait separated it from Asia for even longer periods during interglacials. Throughout the Pleistocene, any oestrid parasite would be forced to pass hundreds of generations in Beringia, where conditions during full-glacial periods, when mammals had free access to Beringia from Asia, would have been particularly severe. It is perhaps not surprising that the fauna of Central Asia, especially if it is of relatively recent origin (post-Miocene), has not been able to follow potential hosts into North America through Beringia.

Further resolution of these problems awaits studies elucidating the phylogenetic relationships and host specificities of all oestrids.

Keys to genera

Adult

1. M fairly straight, terminating well behind wing apex; crossvein dm-cu displaced basally nearly to level of crossvein r-m, or absent (Fig. 5) .... ***Gasterophilus*** Leach

   4 spp., equine stomach bots; all introduced from Europe, now widespread in U.S.A. and southern Canada; Hadwen and Cameron 1918, Cameron 1931

   M curved or sharply angled forward, terminating in front of wing apex; crossvein dm-cu closer to wing margin than to crossvein r-m (Figs. 6–8) 2

2. M terminating in R_{4+5} before reaching wing margin (Fig. 6). Fronto-orbital hairs each arising from a black flat-bottomed pit; hairs of scutum each arising from a small black pustule (Fig. 1) .... ***Oestrus*** Linnaeus

   1 sp., *ovis* Linnaeus, sheep nose bot; introduced from Europe, now widespread in U.S.A. and southern Canada

   M terminating in wing margin (Figs. 7, 8). Hairs of fronto-orbital plate and scutum not arising from pits or pustules 3

3. Head very broad, wider than thorax (Fig. 2). Scutum with short appressed pile; scutellum strongly projecting, shelf-like, over subscutellum (Fig. 9) .... ***Cuterebra*** Clark

   34 spp., rodent and rabbit bots; U.S.A. and southern Canada; Sabrosky 1986

   Head smaller, narrower than thorax. Scutum with long erect pile; scutellum not projecting over subscutellum more than twice its width (Fig. 10) 4

4. Face abruptly narrowed, its lateral margins converging below antennae (Fig. 3). M beyond crossvein dm-cu with a distinct right-angled bend and short extension (Fig. 7) .... ***Cephenemyia*** Latreille

   5 spp.; widespread; Bennett and Sabrosky 1962

   Face broad and shield-like, its lateral margins nearly parallel (Fig. 4). M beyond crossvein dm-cu nearly straight, without a bend (Fig. 8) .... ***Hypoderma*** Latreille 5

5. Palpus absent. Presutural and postsutural areas of scutum each with two pairs of raised shiny black longitudinal stripes .... ***Hypoderma*** (***Hypoderma*** Latreille)

   2 spp., cattle warble fly; both introduced from Europe, now widespread in U.S.A. and southern Canada; Hadwen 1919

Palpus present, as a small black sphere. Presutural and postsutural areas of scutum with median markings almost obliterated .... ***Hypoderma*** (***Oedemagena*** Latreille)
1 sp., *tarandi* (Linnaeus), caribou warble fly; Arctic and Subarctic Canada and Alaska

Larva

(except first instar)

1. Mandible minute, rudimentary, concealed within gullet. Found in cutaneous cysts or warbles, usually on backs of cattle or caribou .... ***Hypoderma***

Mandible well-developed, sharp, curved, usually prominently exerted. Found in nasal passages of sheep or deer, in gut of horses, or in cutaneous warbles of rodents or lagomorphs 2

2. Posterior spiracle with two (second instar) or three (third instar) straight or slightly curved parallel slits, each with ladder-like crossbars (Fig. 19); anterior spiracle a relatively large finger-like process, covered with rows of pores, retracted out of sight in larva (Fig. 18) but everted at puparium formation. Found in gut of horses .... ***Gasterophilus***

Posterior spiracle with either two nonparallel dissimilar slits, or with a sieve plate of numerous closely packed serpentine slits or randomly arranged pores (Figs. 20, 21) 3

3. Integument evenly and densely covered with flattened overlapping scale-like plates or broad conical spines. Posterior spiracle with three pairs of closely intertwined serpentine slits (Fig. 20). Found in subcutaneous cysts of rodents or lagomorphs .... third instar of ***Cuterebra***

Integument with smaller sharp spines arranged in rows or patches that are not completely covering each segment nor overlapping 4

4. Posterior spiracle of two minute dissimilar slits; median slit fairly straight; lateral slit serpentine. Middle abdominal segments each with an anterior band of backwardly directed spines and a posterior band of anteriorly directed spines; these bands separated by a transverse bare area. Found in subcutaneous cysts of rodents and lagomorphs .... second instar of ***Cuterebra***

Posterior spiracle a subcircular sieve plate, with a prominent circular scar of previous-stage spiracle in or near its center (Fig. 21). Dorsum of segment 8 forming a semicircular hood over posterior spiracles, and bearing a prominent shelf-like extension ventral to them (Fig. 21). Found in nasal passages of sheep, goats, and cervids 5

5. Abdominal segments with numerous spines more or less in equal numbers dorsally as well as ventrally. Anterior spiracle small but exerted. Found in cervids such as deer, moose, wapiti, and caribou .... ***Cephenemyia***

Abdominal segment with spines confined to ventral surface. Anterior spiracle virtually indistinguishable. Found in frontal sinuses of sheep and goats .... ***Oestrus***

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SARCOPHAGIDAE 108

G. E. SHEWELL

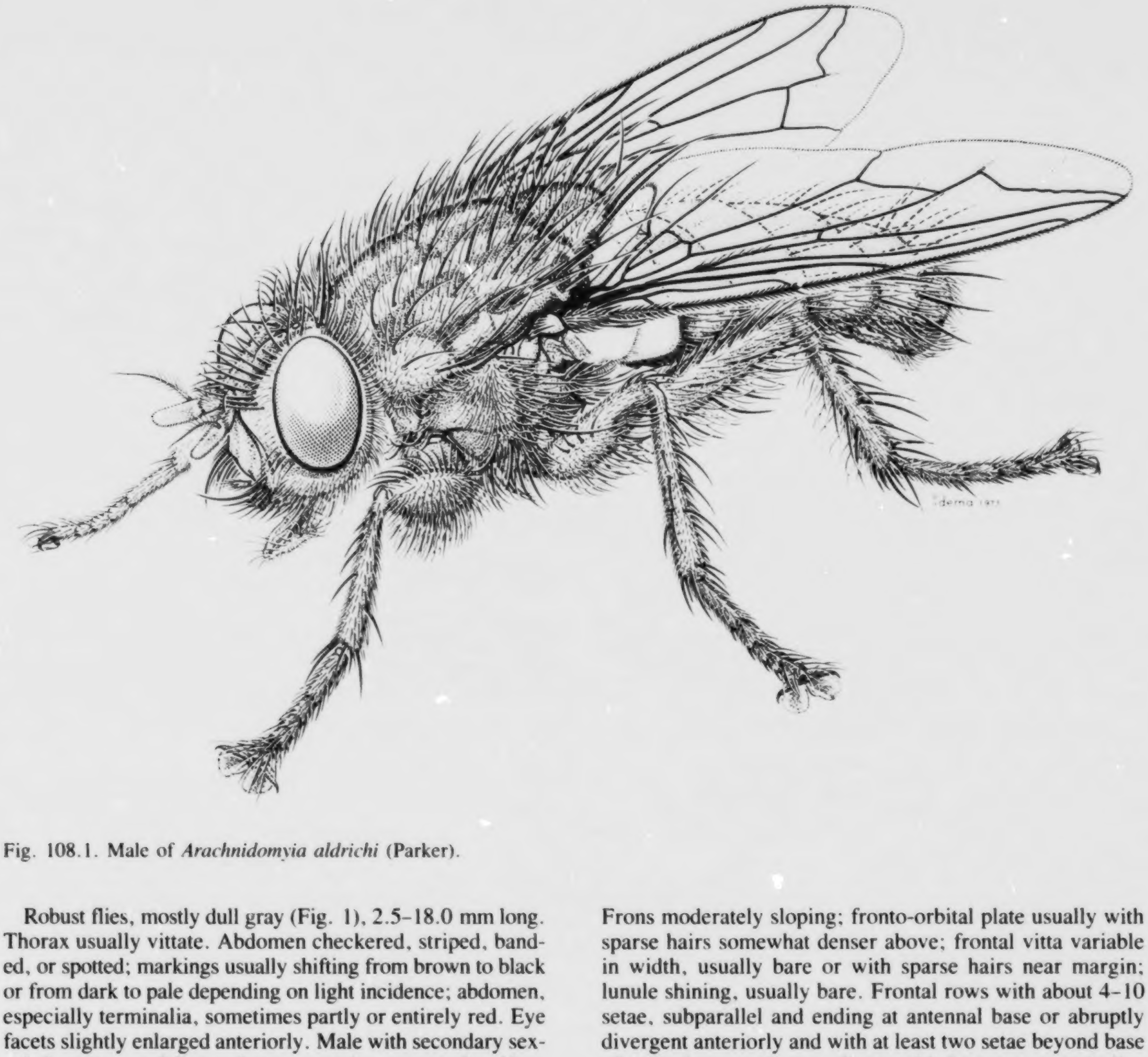


Fig. 108.1. Male of *Arachnidomyia aldrichi* (Parker).

Robust flies, mostly dull gray (Fig. 1), 2.5–18.0 mm long. Thorax usually vittate. Abdomen checkered, striped, banded, or spotted; markings usually shifting from brown to black or from dark to pale depending on light incidence; abdomen, especially terminalia, sometimes partly or entirely red. Eye facets slightly enlarged anteriorly. Male with secondary sexual characters as follows: frons somewhat narrowed, seldom with proclinate orbital or outer vertical setae except in Miltogrammini; thoracic setae and pile often longer, finer, and more erect; middle and hind legs sometimes villous (Fig. 38); anterior tarsus occasionally ornamented (Figs. 100, 101). Claws and pulvilli elongate in male, seldom so in female; sexes sometimes with different body color.

Adult. Head (Figs. 2–22, 80–97): about as wide as thorax, wider than high, usually less than one-third higher than long, in profile subquadrate or triangular; vibrissal axis usually shorter than antennal axis, its angle seldom strong. Frons moderately sloping; fronto-orbital plate usually with sparse hairs somewhat denser above; frontal vitta variable in width, usually bare or with sparse hairs near margin; lunule shining, usually bare. Frontal rows with about 4–10 setae, subparallel and ending at antennal base or abruptly divergent anteriorly and with at least two setae beyond base of pedicel; one to three reclinate orbital setae present, in line with or slightly outside frontal row; two to four proclinate orbital setae present, always well outside other rows, frequently absent in male Sarcophaginae; ocellar setae hair-like to strong; outer vertical seta usually missing in male Sarcophaginae; postocellar setae weak, parallel or divergent; paravertical setae slightly medioclinate. Face concave, not carinate, sometimes strongly retreating, seldom extended much below vibrissae; facial ridge usually haired on less than lower half, rarely setose on whole length (Fig. 95). Parafacial bare to sparsely haired, often with stronger setulae below, sometimes strongly setose along facial margin. Genal groove variable in extent, usually bare; gena haired, with ventral margin rounded or slightly angulate; postgena often pale-haired. Postcranium usually convex, sometimes bulging below (Fig. 19); intrapostocular setulae absent; one to three rows of short setae behind fringe above; supracervical area bare. Antennal scape very short, flush with lunule; pedicel short; first flagellomere up to six times length of pedicel, rarely reaching vibrissae; arista bare to plumose. Proboscis short; labella fleshy; palpus black or yellow, slightly clavate, seldom short filiform or absent (Fig. 95).

Thorax: middle of propleuron usually bare; prosternum and metasternal area bare in Miltogramminae, sparsely haired in Sarcophaginae (Fig. 25); postalar wall haired (Fig. 23) or bare (always bare in Miltogramminae); postnotum with hairs on anatergite (Fig. 23, infrasquamal hairs) except in Miltogrammini. Presutural acrostichal setae usually absent, rarely strong; postsutural acrostichal setae usually limited to prescutellar pair; dorsocentral setae usually arranged 3–4 + 3–4; if more than four postsutural setae present, then anterior ones much weaker; intra-alar setae arranged 1–2 + 1–2; supra-alar setae arranged 1–2 + 3; anterior presutural supra-alar (outer posthumeral) seta, if present, in line with following setae and further from notopleural suture (Fig. 24); two to four postpronotal (humeral) setae present; two notopleural setae present in Miltogramminae (Fig. 98), four in most Sarcophaginae (Fig. 24); two postalar and two or three lateral scutellar setae present; apical scutellar setae, if present, usually small; one discal scutellar seta present. Proepisternal and proepimeral setae present, often with supplementaries; anepisternum often with short upcurved setae above and with a series of five to eight setae on the posterior margin, of which the upper two are declinate; two to three katepisternal setae arranged in straight line or with middle seta slightly lower, seldom forming triangle; anepimeron with strong setae and cluster of hairs above, often bare or only sparsely haired below; anatergite sometimes with a cluster of fine hairs (infrasquamal setulae). Greater ampulla reniform. Coxopleural streak present in Miltogramminae (Fig. 98), absent in Sarcophaginae. Spiracles small, usually pale whitish or brownish; anterior one not filling its sclerite; posterior one subtriangular, with narrow anterior valve plate and larger hinged plate behind; ventral margin without upcurved hairs overlying plates.

Base of wing with tympanic pit, suprasquamal ridge, calypteres, stem vein, and subcostal sclerite bare. R_1 and CuA_1 sometimes setose; node of R_{4+5} setose above and below, with setae continued toward crossvein r-m above. Costal spine sometimes present (Fig. 29). Extension at angle of M (stump vein) seldom well-developed (Fig. 103), usually present as short fold darkened by more numerous microtrichia (Figs. 29–32).

Fore femur with complete posterodorsal and posteroventral rows of setae, sometimes with supplementary row especially above. Fore tibia with weak anterodorsal row usually ending at middle; rarely continued beyond middle third (compare Calliphoridae, Ch. 106); apical dorsal seta present; apical anterodorsal seta weak or absent; one or two posterior or posteroventral setae near middle; apical posteroventral and usually also posterodorsal seta present. Middle femur with short anterior row of setae at middle and diagonal posterodorsal row apically, otherwise bare except for sparse anteroventral and posteroventral rows on basal half; posterior surface sometimes with bare shining striated sensory area in female Sarcophaginae (Fig. 37); apical posteroventral ctenidium present in male of Paramacronychiini and some tribes of Sarcophaginae (Figs. 33–35, 99). Middle tibia usually with one or two anterodorsal setae at middle and one anteroventral or ventral seta at apical third (sometimes absent in male); a single posterodorsal seta present opposite lower anterodorsal seta, and two posterior setae present, the second of which lies close to the posterodorsal seta; apex usually with five or six setae; apical posterodorsal seta weak or absent. Hind femur with complete anterodorsal row and often with supplementary row in Sarcophaginae; anteroventral and posteroventral rows sparse, weak, usually confined to basal half, sometimes absent in male; usually a stronger anteroventral seta present near apical third; single preapical dorsal and posterodorsal setae sometimes present. Hind tibia with two or three anterodorsal and posterodorsal setae on middle third, former often with weaker interspersed supplementaries; one strong and one or two weaker anteroventral setae present at or before apical third; apex with dorsal, anterodorsal, and anteroventral setae present; posterodorsal and posteroventral setae frequently weak or absent. A small bulla (cicatrix) on dorsal ridge near base in some Sarcophaginae.

Abdomen: five segments preceding terminalia and two to four genital segments present. Tergites 1–5 large, with tergites 1 + 2 combined. Sternites 1–4 exposed and overlapping their tergites in male of Sarcophaginae; sternite 5 mostly concealed, its posterior margin strongly bilobate (Figs. 40*a*, 41*a*); sternites 1 and 2 exposed and remainder concealed at least laterally in male of Miltogramminae (Fig. 4); sternite 5 with straight or only shallowly indented hind margin; sternites 1 and 2 exposed and remainder more or less concealed in all females. Spiracles 1–5 small, located ventrally in tergites, usually remote from margins.

Female viviparous, rarely ovoviviparous (*Ptychoneura* Brauer & Bergenstamm). Terminalia short (Figs. 63–79, 105), usually not much concealed by retraction. Tergite 6 sometimes narrowly divided by membrane above (Figs. 63, 65, 66); tergite 7 frequently absent, seldom complete dorsally (Fig. 64); tergite 8 nearly always present but usually reduced to bare shining lateral plates (Figs. 68, 69); epiproct very small, often mainly membranous, with a single pair of setae. Sternites 6 and 7 usually wider than 5; sternite 8 smaller, often membranous, sometimes fused with preceding sternite or sternites and sharpened or tapered for larviposition (Figs. 70, 71, 73); hypoproct always weakly sclerotized, rounded or scutate, usually with covering of fine short hairs. Cercus short. Spiracle 6 situated either within its tergite or in membrane near its anterior margin, rarely in tergite 5 near posterior margin where it may be mistaken for a setal scar, e.g. *Comasarcophaga* Hall (Fig. 74) and *Thelylepticocnema* Townsend; spiracle 7 situated in tergite 6 laterally or in membrane behind it, rarely in well-developed tergite 7, e.g. *Macronychia* Rondani and *Oebalia* Robineau-

Desvoidy (Fig. 105). Three spermathecae present, ovate, pyriform, or elongate, sometimes one smaller; segmental constrictions sometimes pronounced.

Male terminalia (Figs. 39–62, 106) often large, seldom hidden. Tergite 6 reduced (Miltogrammini) or, if absent, usually replaced by extensive membrane; sternite 6 strongly sclerotized, bare, narrow U- or V-shaped with right arm much reduced or even detached from base; spiracle 6 situated in membrane laterally near margin of following segment. Combined segments 7 + 8 forming arched dorsal plate closely attached to following tergite, often asymmetric with rows of setae or with grooves indicating segmental fusion, bearing spiracle 7 laterally. Epandrium usually about equal to preceding segment, occasionally incomplete (membranous) above, rarely with strong setae. Cerci rigid, either forcipate and juxtaposed or else greatly modified, strongly bent back, explanate, notched, denticulate, or spinose, rarely fused together. Surstylus articulated, either rigid and elongate (Miltogramminae) or weakly sclerotized, shortened, lamellate or papillate (Sarcophaginae). Hypandrium trough-shaped; gonopod more or less fused to hypandrium; paramere free-moving; bacilliform sclerite often rudimentary, if complete usually short; aedeagus with or without distinct basiphallus; either epiphallus present and distiphallus simple with opening of sperm duct membranous and exposed (Miltogrammini) or epiphallus reduced or absent and distiphallus enlarged and complex with opening of duct concealed within sclerotized acrophallus (juxta) and often surrounded by paired appendages, including dorsoapical processes called copi (Roback 1954) (Paramacronychiini, Sarcophaginae); aedeagal apodeme elongate; ejaculatory apodeme sometimes large (Fig. 58).

Egg. Length 0.5–3.5 mm, width 0.12–0.8 mm. In nearly all cases, hatching seems to occur within the uterus, at or just before larviposition. Therefore published descriptions of the egg are rare. Hinton (1981) illustrates some surface features of eggs of *Neobellieria bullata* (Parker) under high magnification and says that they resemble those of Calliphoridae (Ch. 106).

Larva. White or pale yellowish, usually elongate cylindrical, tapered anteriorly, sometimes fusiform, rarely dorsoventrally compressed with intersegmental constrictions (*Colcondamyia* Reinhard). Segments, except first, with more or less complete anterior and posterior bands of hairs, spines, or denticles, sometimes also with lateral spine patches or scattered denticles (*Brachicoma* Rondani, *Servaisia* Robineau-Desvoidy, *Cistudinomyia* Townsend) (Figs. 111–113). Posterior spiracular field sunken in cavity, especially in later instars. Cephalopharyngeal skeleton large; mandible usually strong, hook-like, sometimes rudimentary in first instar (Miltogramminae).

First instar 0.5–5.0 mm long. Miltogramminae with labral sclerite developed as a strong median hook; mandibular sclerites reduced to small basal plates and slender apical rods with serrated tips (Figs. 109–110). Sarcophaginae with labral sclerite absent or reduced to small triangular plate between bases of strong mandibles (Figs. 107, 108); first segment sometimes sclerotized dorsally, forming a partial head capsule (*Titanogrypa* Townsend); hypopharyngeal sclerite present, sometimes fused with tentoropharyngeal sclerite; tentoropharyngeal sclerite usually large, sometimes without dorsal bridge or ocular depression; anterior spiracle absent; posterior spiracle bilobate or, rarely, bispinose, with possibly two poorly defined oval apertures; felt chamber sometimes long and slender.

Second instar 4.0–10.0 mm long. Similar to third instar but posterior spiracle with only two openings.

Third instar (Figs. 114–116) 9.5–20 mm long. Mandible large, more or less strongly curved; dorsal cornu of tentoropharyngeal sclerite appearing deeply incised because of presence of narrow apical window (Fig. 114). Anterior spiracle with short stalk bearing 9–20 or more nodular branches arranged fan-wise. Posterior spiracle with three narrow subparallel vertical opening slits surrounded by peritreme (Fig. 116). Spiracular disc sunken within oval cavity (except *Macronychia* and some species of *Amobia* Robineau-Desvoidy) around which are 8–12 tubercles in two groups of three dorsally and two to six ventrally; dorsal tubercles sometimes sclerotized and dentate; ventral tubercles often mammillate. Anal opening in more or less prominent posteroventral lobe bearing lateral tubercles (Fig. 115).

Biology and behavior. Female Sarcophagidae are without exception viviparous or ovoviviparous. Larvae of most Miltogrammini are laid at or near the entrance to nests of burrowing Hymenoptera. They develop as inquilines in the brood cells, feeding on the provisions and sometimes destroying the egg or larva of the host. In *Ptychoneura*, which attacks stem-nesting Hymenoptera, fully incubated eggs are deposited on the female host as she enters the nest hole (Day and Smith 1981). Other exceptions are *Hilarella* Rondani, reared from Orthoptera (Arnaud 1954); *Eumacronychia* Townsend, parasitizing turtle and lizard eggs; and *Macronychia*, parasitizing adult Tabanidae (Lopes 1982, Mullen *et al.* 1984, Thompson 1978).

Knowledge of the biology of this tribe comes mainly from workers studying the habits of wasps and bees (Krombein 1953, 1955, 1963, 1964), but a primary study was also done by Moradeshaghi and Bohart (1968) on *Euphytomima nomiivora* Reinhard living in nests of the alkali bee, *Nomia melanderi* Cockerell. These authors constructed artificial brood cells furnished with pollen balls of the host. Larvae extracted from female flies and placed in the cells developed to maturity on the pollen. Pupation in this and other observed species occurred in the soil some distance from the host burrow.

Habits of Paramacronychiini and Sarcophaginae are more varied, but the known hosts of the parasitic forms are mostly insects and other arthropods. Numerous species in eight tribes have been reared from Orthoptera, Coleoptera, and Lepidoptera, fewer from Neuroptera, Homoptera, and Hymenoptera; but although some species are certainly obligate parasites, others appear to be primarily scavengers that become facultative parasites in favorable circumstances. A few species in three tribes parasitize spiders, myriopods, and scorpions. Species of Johnsoniini, Microcerellini, and Sarcodexiini attack land snails. *Cistudinomyia* is a subcutaneous parasite of land turtles, and *Anolisimyia* Dodge has been reared from a chameleon. James (1947) lists six Nearctic sarcophagids implicated in cutaneous myiasis in humans, but all except *Wohlfahrtia* Brauer & Bergenstamm are believed to be secondary invaders of wounds and sores. *Wohlfahrtia* spp. larviposit on the healthy young of domestic and wild animals and on human infants. The larva breaks the skin and feeds subcutaneously, producing a furuncular sore. Babies left outdoors in prams and unprotected by netting are common victims. Degree of cleanliness is not a factor in susceptibility, exposure being all that is necessary. According to Haufe and Nelson (1957) attacks are restricted to children well under one year, the skin later becoming too strong for larval penetration. Some Parasarcophagini and most Raviniini appear to be scatophagous, and a few of them are cited in medical records as causing intestinal myiasis usually on the basis of live maggots being found in the stools of patients. Many such reports, however, are thought to involve contamination of stools after defecation. According to James (1947), only one species, *Bercaea haemorrhoidalis* (Fallén), is reliably recorded as developing in the human digestive tract after being ingested on contaminated food. The presence of larvae in the tract causes pain, nausea, vomiting, and fever.

Because their biological association with humans is limited, Sarcophagidae have not achieved the same notoriety as pests as have some Calliphoridae. One beneficial species, *Arachnidomyia aldrichi* (Parker), is a major natural control agent for the forest tent caterpillar, *Malacosoma disstria* Hübner, which it attacks in the pupal stage (Hodson 1941, Arthur and Coppel 1953). Male Sarcophaginae frequently visit flowers, but females of many species must be bait-trapped or searched for near their hosts. Miltogrammini of both sexes are usually found on bare soil, or sunning on stones, in sandy waste places frequented by burrowing Hymenoptera. When disturbed, they fly short distances, rising only an inch or two from the ground.

Classification and distribution. Earlier writers on this family used *Sarcophaga* Meigen in the broadest sense when describing new species. Aldrich (1916) made no subfamily or tribal divisions. He assumed that genera with bare arista belonged in the Tachinidae, and it was not until Baer (1921) and Malloch (1923) had drawn attention to the exclusive tachinid character of enlarged subscutellum that Allen (1926) was able to bring together and revise the Miltogrammini. Townsend's *Manual of Myiology* (Townsend 1935–1938) did not clarify subfamily and tribal associations within the group, but in fact added to the problem by dispersing Aldrich's genera as well as many of his own segregates from the old genus *Sarcophaga* among five tribes that clearly were mixtures of both Miltogramminae and Sarcophaginae. Lopes (1939, 1943, 1946, 1950, 1956*a,b*) in Brazil began a series of studies on the Neotropical fauna, applying Townsend's genera as much as possible, with redescriptions accompanied by detailed figures, also including Nearctic species in some cases. His classification (Lopes 1969) recognizes four subfamilies, splitting Miltogramminae into two groups and raising Paramacronychiini to subfamily status. His tribes of Sarcophaginae are difficult to assess because of the many extralimital genera. However, his Sarcophagulini is the same as Sarothromyiini of the present work, and Raviniini is also the same in both. His Tephromyiini corresponds to Protodexiini plus Impariini. He does not go as far in dividing Sarcophagini. The work of Roback (1954) is important because of its careful and detailed analysis of the internal structure of the aedeagus, supplemented by drawings of nearly 150 species. The validity of his classification, based on the presumed evolution of this organ from a hypothetical ancestral (muscoid) type, cannot be fully assessed. However, on the basis of other characters used in the present treatment, there is full agreement in Roback's subtribe Raviniina and partial correspondence in subtribes Boettcheriina and Servaisiina. Downes (1955) placed the higher classification for the first time on a sound footing. Using new characters of both adult and first-stage larva, this author clearly showed that Miltogrammini and Paramacronychiini should be combined in a single subfamily as a sister group of Sarcophaginae. Downes' characters are valid for the Old World fauna. The present treatment retains his concept while attempting a new tribal arrangement of Sarcophaginae based on characters of both sexes supplemented by those of the first-stage larva where available. The work of European authors has also been consulted, especially the Palaearctic classification of Rohdendorf (1937, 1965). Differences in the first-stage larvae provide valuable clues to relationships in this family, but up to now very little attention has been paid to them. Thompson (1921) made useful studies on Old World Miltogramminae. The study by Knipling (1936) and many papers of Lopes provide a basis for further work on this continent.

The family is almost world wide with over 2000 described species in nearly 400 genera, most of them tropical to warm temperate. Few species occur in high northern latitudes, only three being known from tundra areas in the Mackenzie River Delta, and none from the Arctic islands or Greenland. Southeast Asia and Australia also have limited faunas and there are so far no published records of endemic species in New Zealand, the single common species there being an immigrant from South America. Some widespread synanthropic species range through the Pacific islands, and Hawaii has several North American immigrants. Important from an evolutionary standpoint are the marked distributional differences between the two subfamilies. In Sarcophaginae, the New World fauna exceeds that of the Old World in numbers of genera and species. The Neotropical region is by far the richest with nearly 600 species. Next highest are the Palaearctic region with 300 and the Nearctic region with nearly 250. The opposite holds for the Miltogramminae, in which both Palaearctic and Afrotropical faunas greatly outnumber all the others. Only 43 miltogrammines have been described from South America. There is also a marked difference in faunal relationships. Whereas Miltogramminae show a rather strong Holarctic distribution pattern, this is very much less evident in Sarcophaginae. The tribes of Nearctic Sarcophaginae are preponderantly Neotropical, probably in origin, certainly in affinity. No fossil Sarcophagidae have been reported, but biological and distributional data suggest they are younger than both the Calliphoridae and the Tachinidae.

Key to genera

1. Arista usually plumose (Figs. 5–10, 12–15, 18–22), but if pubescent or bare (Figs. 11, 16, 17), then hind coxa with fringe of hairs on posterior margin (Fig. 23). Coxopleural streak absent (Fig. 23). Cephalopharyngeal skeleton of first-instar larva with two mandibular hooks (Figs. 107, 108) .... SARCOPHAGINAE....2

Arista usually bare or pubescent (Figs. 82–95), but if short plumose, then hind coxa bare on posterior margin. Coxopleural streak present (Fig. 98). Cephalopharyngeal skeleton of first-instar larva with a single labral hook (Figs. 109, 110) ...MILTOGRAMMINAE....66

2. Postalar wall haired in middle (Fig. 23) 3

Postalar wall bare 51

3. Frontal rows of setae parallel, ending level with antennal base or with a single seta below it (Figs. 3, 6). Parafacial hairs scattered, not in single row near eye (Fig. 6). If frontal rows evenly divergent, then parafacial bare or almost so (Figs. 4, 7)......RAVINIINI....4

Frontal rows of setae abruptly divergent at antennae (Fig. 2). At least two setae below level of antennal base (Fig. 5). If rows parallel and ending at antennae, then parafacial with conspicuous row of hairs near eye 9

4. Tegula pale ....***Ravinia*** Robineau-Desvoidy

17 spp.; widespread; Hall 1928, Dodge 1956*a*

Tegula black 5

5. R_1 setose ....***Argoravinia*** Townsend

1 sp., *modesta* (Wiedemann); Texas, Louisiana

R_1 bare 6

6. One or two pairs of presutural acrostichal setae present. Terminalia black (Fig. 41) ....***Dexosarcophaga*** Townsend

1 sp., *transita* Townsend; Texas

Presutural acrostichal setae usually absent. Terminalia at least partly red 7

7. Palpus reddish brown. Gena about half height of eye ....***Cistudinomyia*** Townsend

1 sp., *cistudinis* (Aldrich); central and south U.S.A.

Palpus black. Gena about one-fourth height of eye 8

8. Hairs of gena and postgena mostly white. Apical scutellar setae present in both sexes. Mid femur without ctenidium (Fig. 36) ....***Chrysagria*** Townsend

1 sp., *duodecimpunctata* Townsend (=*tenta* Hall); Florida

Hairs of gena and postgena mostly black. Apical scutellar setae absent in female and usually in male also. Mid femur of male with ctenidium (Fig. 34) ...***Oxysarcodexia*** Townsend

10 spp.; widespread; Lopes 1946, Dodge 1966

9. Hairs on upper part of parafacial scattered (Fig. 5), not in single row close to eye, or if so, then gena entirely pale-haired 10

Parafacial above with single row of hairs close to eye (Fig. 10). Gena entirely or mostly black-haired 26

10. Prosternum broad (Fig. 28) .........................EMBLEMASOMATINI....11

Prosternum narrow (Fig. 25) 12

11. Four postsutural dorsocentral setae decreasing in size anteriorly. Lower margin of head retreating; vibrissal angle not prominent; face greatly extended below vibrissa (Fig. 8). Tergite 5 red, at least on hind margin ....***Emblemasoma*** Aldrich

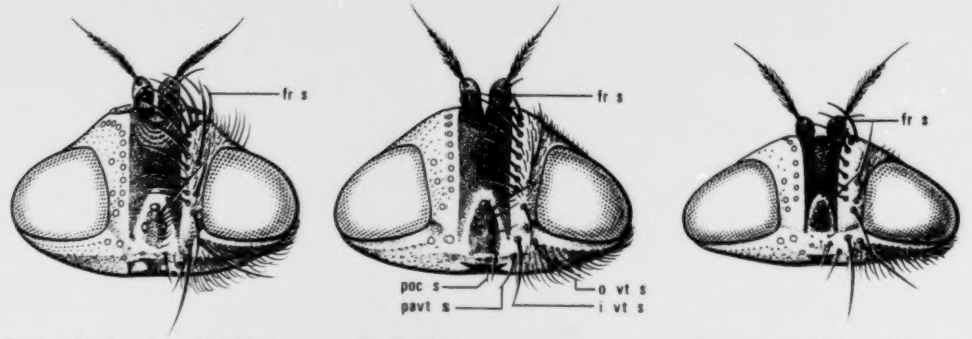
3 spp.; widespread; Reinhard 1939*b*, Lopes 1971*b*

Three subequal postsutural dorsocentral setae present. Lower margin of head not retreating; vibrissal angle prominent; face not much extended below vibrissa (Fig. 9). Tergite 5 black ....***Colcondamyia*** Reinhard

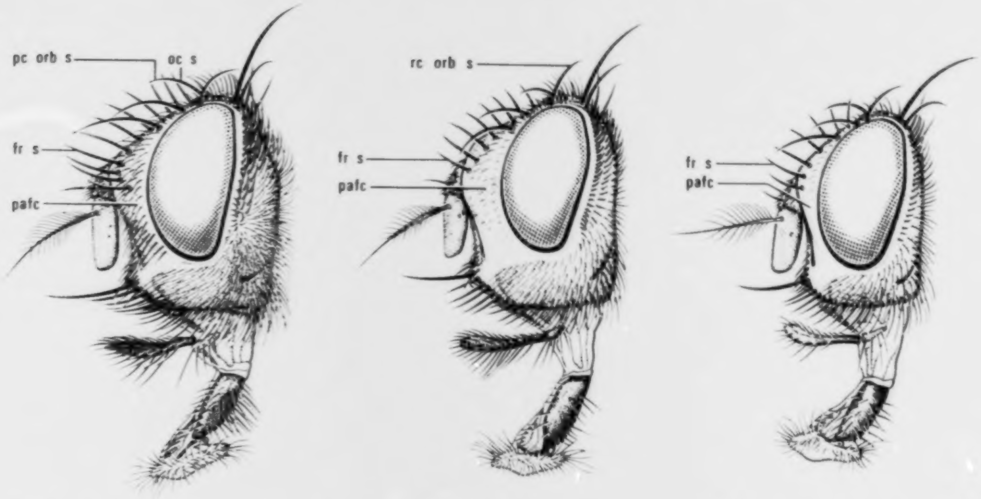
2 spp.; Nevada, Ontario

12. Arista pubescent or short plumose; longest rays at most about half as long as width of first flagellomere (Fig. 11). Costal spine present ..........COMASARCOPHAGINI....13

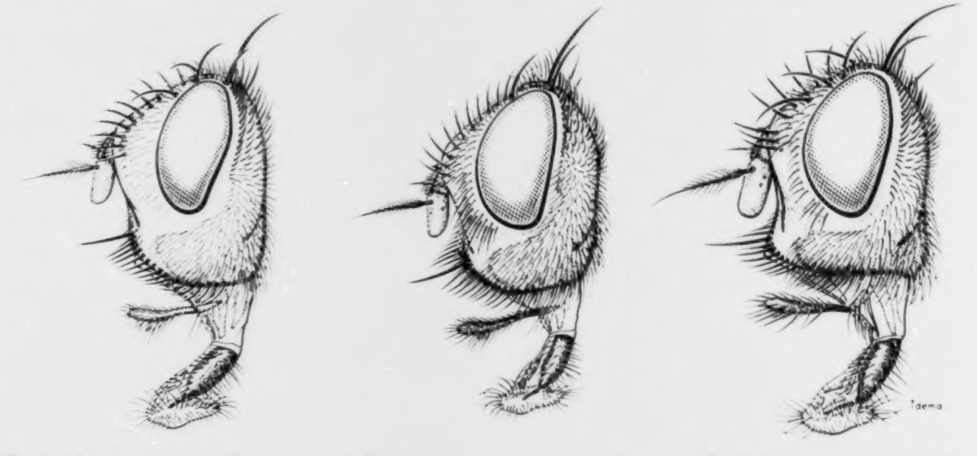
Arista long plumose; longest rays at least as long as width of first flagellomere (Fig. 5). Costal spine absent 14



2 Arachnidomyia aldrichi ♀ **3** Ravinia querula ♀ **4** Oxysarcodexia cingarus ♀



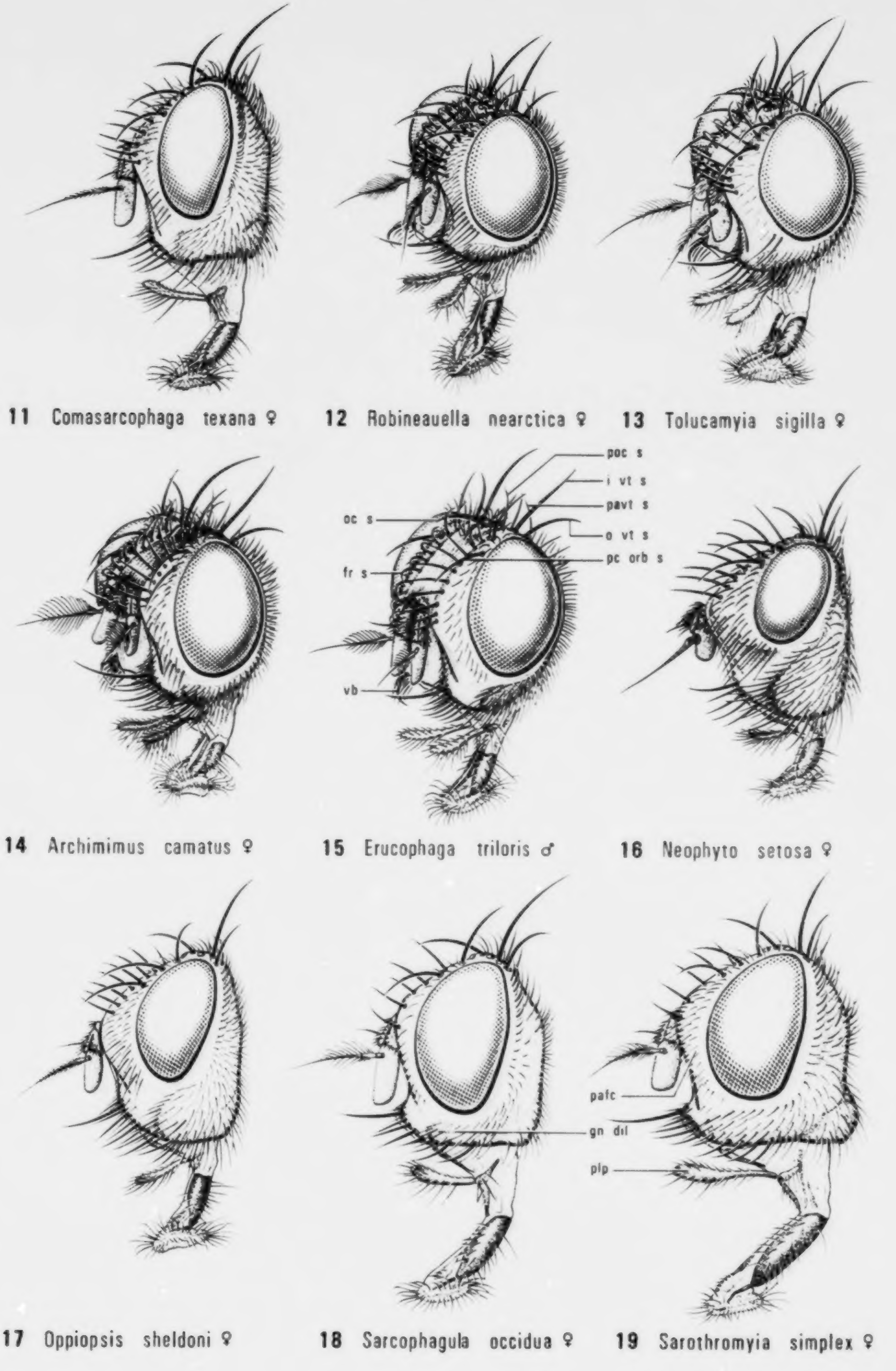
5 Arachnidomyia aldrichi ♀ **6** Ravinia querula ♀ **7** Oxysarcodexia cingarus ♀



8 Emblemasoma erro ♀ **9** Colcondamyia auditrix ♀ **10** Bellieria melanura ♀

Figs. 108.2–10. Heads of Sarcophaginae: dorsal and lateral views of (2, 5) *Arachnidomyia aldrichi* (Parker), (3, 6) *Ravinia querula* (Walker), and (4, 7) *Oxysarcodexia cingarus* (Aldrich); lateral views of (8) *Emblemasoma erro* Aldrich, (9) *Colcondamyia auditrix* Shewell, and (10) *Bellieria melanura* (Meigen) (*continued*).

Abbreviations: fr s, frontal seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; pafc, parafacial; pavt s, paravertical seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; rc orb s, reclinate orbital seta.



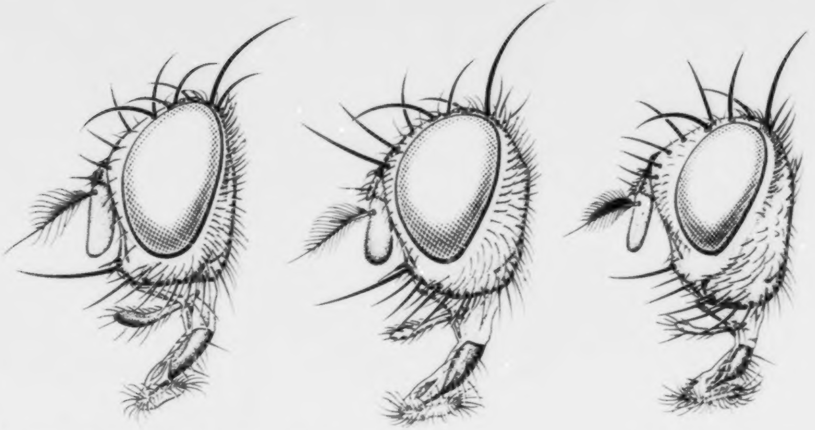
11 Comasarcophaga texana ♀ **12** Robineauella nearctica ♀ **13** Tolucamyia sigilla ♀

14 Archimimus camatus ♀ **15** Erucophaga triloris ♂ **16** Neophyto setosa ♀

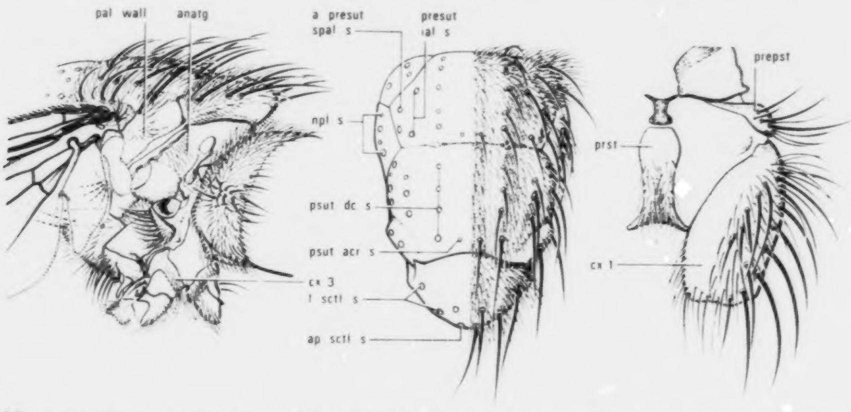
17 Oppiopsis sheldoni ♀ **18** Sarcophagula occidua ♀ **19** Sarothromyia simplex ♀

Figs. 108.11–19. Heads of Sarcophaginae (*continued*): lateral and anterolateral views of (11) *Comasarcophaga texana* Hall, (12) *Robineauella nearctica* (Parker), (13) *Tolucamyia sigilla* (Reinhard), (14) *Archimimus camatus* Reinhard, (15) *Erucophaga triloris* Reinhard, (16) *Neophyto setosa* (Coquillett), (17) *Oppiopsis sheldoni* (Coquillett), (18) *Sarcophagula occidua* (Fabricius), and (19) *Sarothromyia simplex* Aldrich (*continued*).

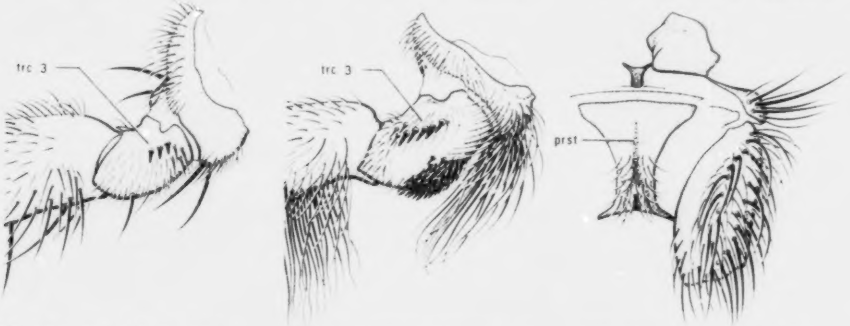
Abbreviations: fr s, frontal seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; pavt s, paravertical seta; pc orb s, proclinate orbital seta; poc s, postocellar seta; vb, vibrissa.



20 Sarcofahrtiopsis paterna ♀ **21** Johnsonia elegans ♀ **22** Camptops unicolor ♀



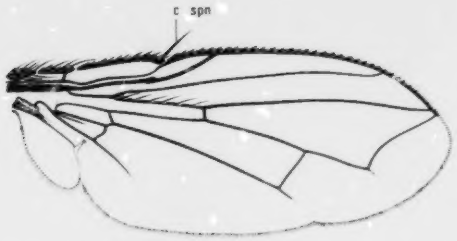
23 Arachnidomyia aldrichi ♀ **24** Arachnidomyia aldrichi ♂ **25** Arachnidomyia aldrichi ♂



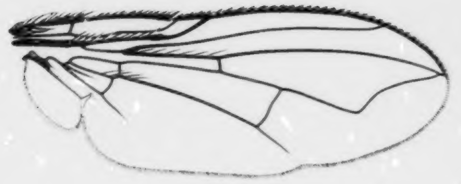
26 Kellymyia plinthopyga ♀ **27** Boettcheria latisterna ♂ **28** Emblemasoma erro ♂

Figs. 108.20–28. Heads of Sarcophaginae (*concluded*) and details of thorax and legs of same: lateral views of heads of (20) *Sarcofahrtiopsis paterna* Dodge, (21) *Johnsonia elegans* Coquillett, and (22) *Camptops unicolor* Aldrich; (23) posterolateral view, with lower calypter cut away, of thorax of *Arachnidomyia aldrichi* (Parker); (24) dorsal view of thorax of *Arachnidomyia aldrichi*; prosternum of (25) *Arachnidomyia aldrichi* and (28) *Emblemasoma erro* Aldrich; posterior view of left hind trochanter of (26) *Kellymyia plinthopyga* (Wiedemann) and (27) *Boettcheria latisterna* Parker.

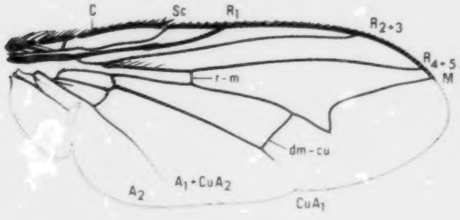
Abbreviations: anatg, anatergite; a presut spal s, anterior presutural supra-alar seta; ap sctl s, apical scutellar seta; cx, coxa; l sctl s, lateral scutellar seta; npl s, notopleural seta; pal wall, postalar wall; prepst, proepisternum; presut ial s, presutural intra-alar seta; prst, prosternum; psut acr s, postsutural acrostichal seta; psut dc s, postsutural dorsocentral seta; trc, trochanter.



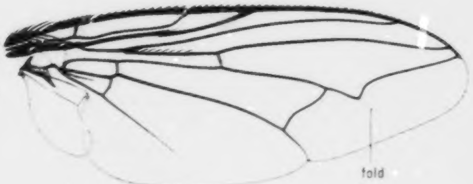
29 Microcerella hypopygialis ♀



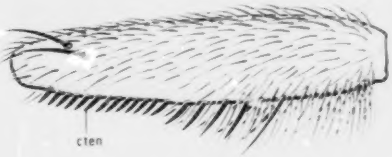
30 Johnsonia elegans ♀



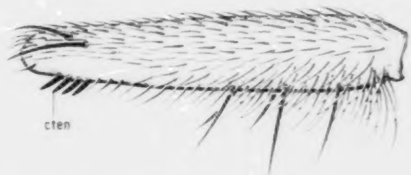
31 Fletcherimyia fletcheri ♀



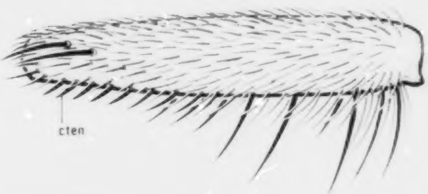
32 Arachnidomyia aldrichi ♀



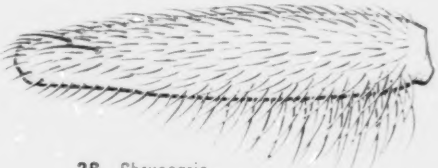
33 Ravinia querula ♂



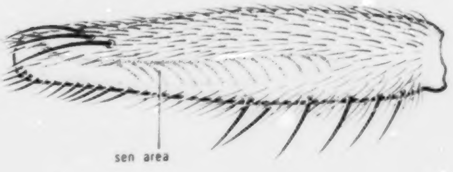
34 Oxysarcodexia cingarus ♂



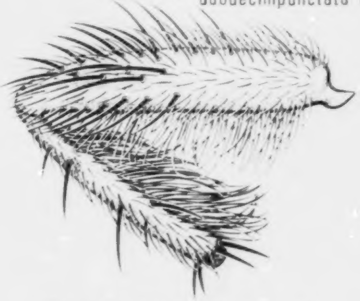
35 Protodexia hunteri ♂



36 Chrysagria duodecimpunctata ♂



37 Arachnidomyia aldrichi ♀



38 Boettcheria latisterna ♂

Figs. 108.29–38. Wings and legs of Sarcophaginae: wings of (29) *Microcerella hypopygialis* (Townsend), (30) *Johnsonia elegans* Coquillett, (31) *Fletcherimyia fletcheri* (Aldrich), and (32) *Arachnidomyia aldrichi* (Parker); posterior views of left mid femur of (33) *Ravinia querula* (Walker), (34) *Oxysarcodexia cingarus* (Aldrich), (35) *Protodexia hunteri* (Hough), (36) *Chrysagria duodecimpunctata* Townsend, and (37) *Arachnidomyia aldrichi*; (38) anterior view of right hind femur and tibia of *Boettcheria latisterna* Parker.

Abbreviations: c spn, costal spine; cten, ctenidium; sen area, sensory area.

13. Ocellar setae much smaller than orbital setae. Apical scutellar setae absent. Terminalia usually brown or black (Fig. 43) .... ***Mecynocorpus*** Roback

1 sp., *salvum* (Aldrich); central and south U.S.A.

Ocellar setae equal to orbital setae. Apical scutellar setae usually present in male. Terminalia red (Fig. 44) .... ***Comasarcophaga*** Hall

2 spp.; Texas, California

14. Three or four evenly spaced postsutural dorsocentral setae distinctly longer than surrounding hairs. Genal hairs black. Female tergite 6 narrowly divided by membrane in middle (Fig. 63) .... SARCOPHAGINI....15

Five or six postsutural dorsocentral setae present, the anterior ones much reduced. Genal hairs often white or pale golden. Female tergite 6 not always divided in middle (Fig. 64) .... PARASARCOPHAGINI....21

15. Pruinescence indistinct or absent on apical fourth or more of each abdominal segment. Syntergosternite 7 + 8 shining, without pruinescence .... ***Neosarcophaga*** Shewell

9 spp.; western

Pruinescence of abdomen reaching hind margins of segments. Syntergosternite 7 + 8 mainly pruinose 16

16. A distinct pair of presutural acrostichal setae present (Fig. 24) .... ***Arachnidomyia*** Townsend

7 spp.; widespread

Presutural acrostichal setae absent 17

17. Parafacial golden pruinose, inconspicuously haired, with only one or two longer hairs below (Fig. 13). Abdominal pruinescence white, changing to yellow posteriorly. Apical scutellar setae absent .... ***Tolucamyia*** Dodge

1 sp., *sigilla* (Reinhard); Arizona, Mexico

Parafacial white or yellowish white pruinose, noticeably haired (Fig. 12). Abdominal pruinescence uniformly white or yellowish white. Male with apical scutellar setae 18

18. Three postsutural dorsocentral setae present .... ***Bercaeopsis*** Townsend

30 spp.; mostly eastern; Dodge 1956*b* (as *Idoneamima* Dodge)

Four postsutural dorsocentral setae present 19

19. Male syntergosternite 7 + 8 with marginal row of setae. Female tergite 6 conically protruding (Fig. 75) .... ***Robineauella*** Enderlein

2 spp.; widespread

Male syntergosternite 7 + 8 without marginal setae. Female tergite 6 with sides curved inwards, not protruding (Figs. 64–66) 20

20. Lobes of sternite 5 of male without spines on inner surface. Female tergite 6 with about eight marginal setae on each side, evenly spaced and about equal in size; hairs moderately long, about half length of setae above. Terminalia red .... ***Sarraceniomyia*** Townsend

1 sp., *sarraceniae* (Riley); widespread

Lobes of sternite 5 of male with heavy spines on inner surface. Female tergite 6 either with 10 or more evenly spaced setae, or with setae confined to dorsal half or less; some hairs above almost as long as setae; rarely all hairs short. Terminalia black or red .... ***Liosarcophaga*** Enderlein

6 spp.; widespread (=*Rosellea* Rohdendorf 1937)

21. Parafacial hairs arranged in single row close to eye. Facial ridge dark, contrasting with pale center of face 22

Parafacial hairs scattered over most of surface, especially above. Facial ridge not noticeably darker than center of face 23

22. Scutellum of male with four pairs of marginal setae, including cruciate apical pair. Ctenidium present .... ***Euboettcheria*** Townsend[1]

1 sp., *volucris* (Wulp); Texas

Scutellum of male with only three pairs of marginal setae, including apical pair. Ctenidium absent .... ***Paraphrissopoda*** Townsend[1]

3 spp.; southern

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[1] Females of *Euboettcheria* and *Paraphrissopoda* are apparently not separable.

23. Gena with white hairs continued to anterior margin, sometimes with some black hairs above. Female tergite 6 dorsally folded but not membranous (Fig. 64) ..... ***Liopygia*** Enderlein
2 spp.; widespread (=*Thomsonea* Rohdendorf 1937 and *Jantia* Rohdendorf 1937)

Gena with black hairs on at least anterior third. Female tergite 6 narrowly membranous on mid-dorsal line (Figs. 65, 66) 24

24. Posterior half of gena mostly white-haired. Male cercus in profile with distinct notch near base on hind margin (Fig. 46). Female tergite 6 polished above, not pruinose; sternite 7 exposed, strongly convex (Fig. 65) .... ***Bercaea*** Robineau-Desvoidy
1 sp., *haemorrhoidalis* (Fallén); widespread

Gena mostly black-haired, but if with pale hairs posteriorly, then male cercus in profile straight or curved and without distinct notch near base. Female tergite 6 usually dull pruinose; sternite 7 either concealed or if partly exposed then flat or slightly concave (Fig. 66) ... 25

25. Palpus usually black; if yellow, then tegula or legs, or both, also yellow. Male with outer vertical setae absent, terminalia red, cercus in profile curved and tapered to point .... ***Neobellieria*** Blanchard
6 spp.; widespread (=*Sapromyia* Roback 1954, and *Robackina* Lopes 1975)

Palpus usually yellow. Male with outer vertical setae present, or if absent, then terminalia black; cercus in profile straight or slightly concave, not tapered; tip with sharp tooth and dense brushes of short erect hairs (Fig. 47) .... ***Wohlfahrtiopsis*** Townsend[2]
4 spp.; mostly southern and southwestern

26. Costal spine present. Terminalia black (Figs. 48, 49). R_1 bare ...... BELLIERIINI 27

Costal spine usually absent, but if present, then either terminalia red or R_1 setose 29

27. Presutural acrostichal setae present .... ***Pierretia*** Robineau-Desvoidy
1 sp., *cockerellae* (Aldrich); western montane

Presutural acrostichal setae absent 28

28. Mid femur anteriorly with all hairs black .... ***Bellieria*** Robineau-Desvoidy
1 sp., *melanura* (Meigen); eastern (immigrant)

Mid femur anteriorly with patch of appressed golden or white hairs near apex .... ***Sarcotachinella*** Townsend
1 sp., *sinuata* (Meigen); widespread

29. Gena with pale hairs on posterior part, or if all hairs black, then R_1 setose. Presutural acrostichal setae absent, or rarely a single weak pair present close to suture, in which case presutural dorsocentral setae not reduced .... SARCODEXIINI 30

Gena with all hairs black; pale hairs confined to postgena. R_1 usually bare. Two or more pairs of presutural acrostichal setae present, usually strong; if weak then presutural dorsocentral setae also weak 34

30. Terminalia black. Tergite 3 with strong median marginal setae. Middle pair of marginal setae on tergite 5 placed farther forward than others .... ***Titanogrypa*** Townsend
2 spp.; widespread east of Rocky Mountains

Terminalia red (Fig. 50). Tergite 3 without median marginal setae; those of tergite 5 in single line 31

31. R_1 bare 32

R_1 setose 33

32. Lateral margin of scutellum with sparse black hairs .... ***Sarcodexia*** Townsend
3 spp.; eastern and southern U.S.A.

Lateral margin of scutellum with dense yellow pile .... ***Cucullomyia*** Roback
1 sp., *pedunculata* (Hall); Texas; Lopes 1976

33. Hairs of gena black. Three postsutural dorsocentral setae present ..... ***Helicobia*** Coquillett
2 spp.; widespread; Lopes 1939

Hairs of gena white posteriorly. Four postsutural dorsocentral setae present, the first two of which are greatly reduced .... ***Tylomyia*** Roback
3 spp.; Texas

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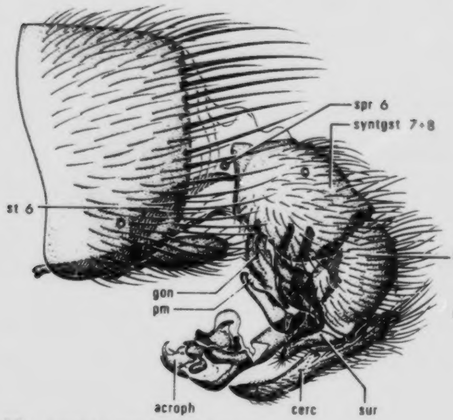
[2] Female of *W. utilis* (Aldrich) has a black palpus and tegula but is distinguished from *Neobellieria* by having tergite 6 polished above.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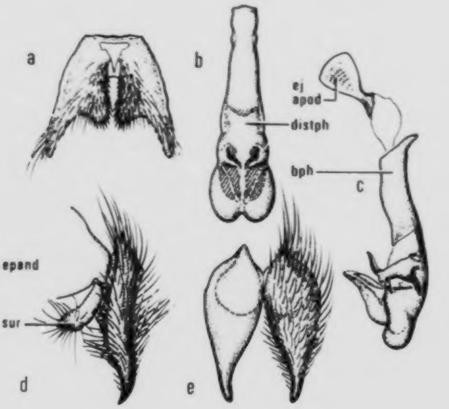
39 Arachnidomyia aldrichi ♂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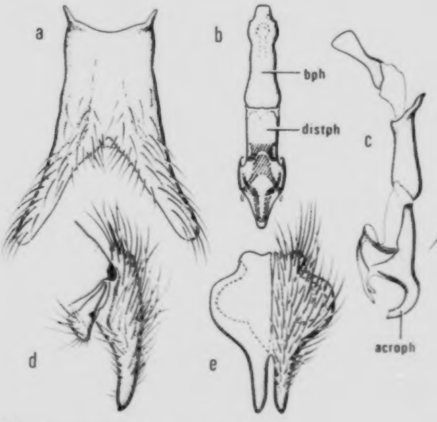
40 Ravinia acerba ♂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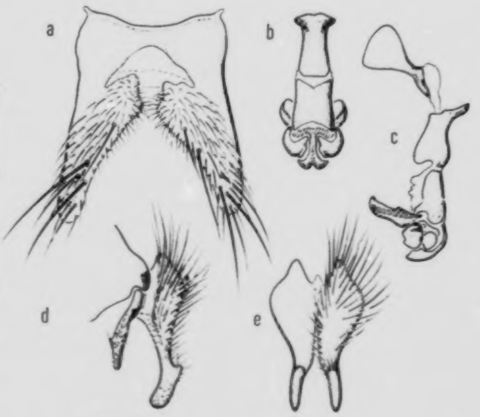
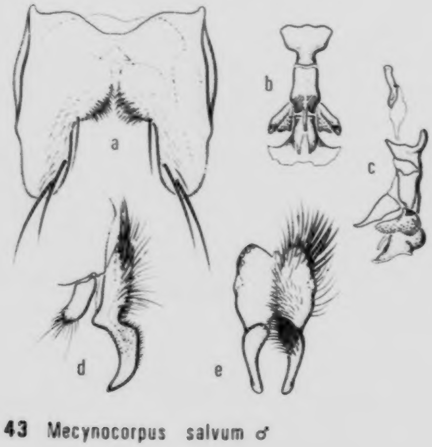
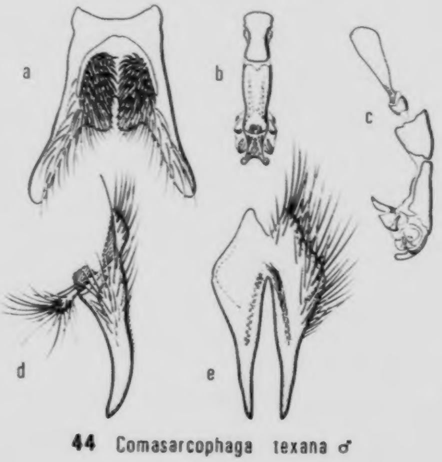
41 Dexosarcophaga transita ♂



42 Emblemasoma erro ♂



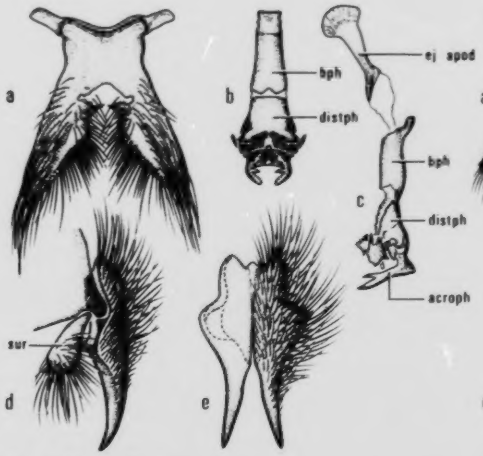
43 Mecynocorpus salvum ♂



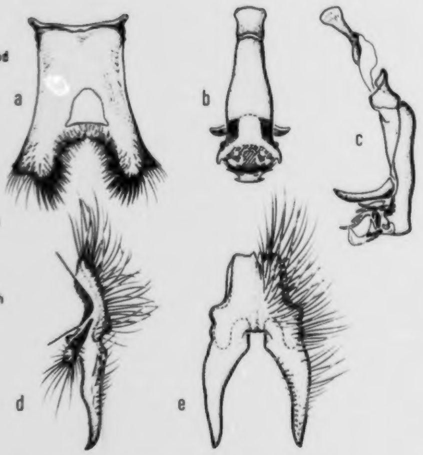
44 Comasarcophaga texana ♂

Figs. 108.39–44. Male terminalia of Sarcophaginae: (39) lateral view of *Arachnidomyia aldrichi* (Parker); parts of terminalia (a sternite 5, b and c posterior and lateral views of aedeagus, d and e lateral and posterior views of cercus and surstylus) of (40) *Ravinia acerba* (Walker), (41) *Dexosarcophaga transita* Townsend, (42) *Emblemasoma erro* Aldrich, (43) *Mecynocorpus salvum* (Aldrich), and (44) *Comasarcophaga texana* Hall (*continued*).

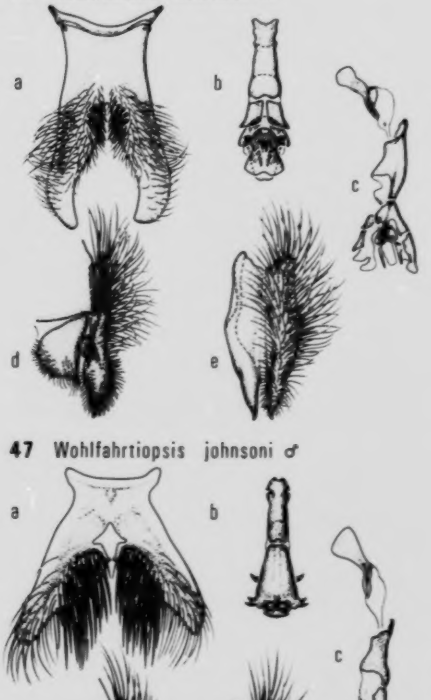
Abbreviations: acroph, acrophallus; bph, basiphallus; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; pm, paramere; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite.



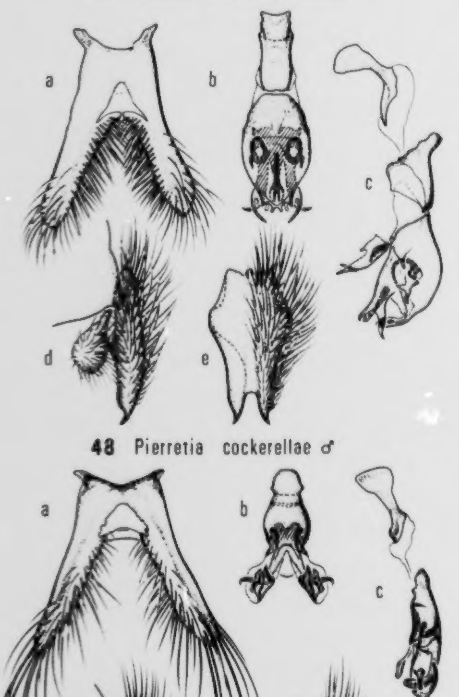
45 Robineauella nearctica ♂



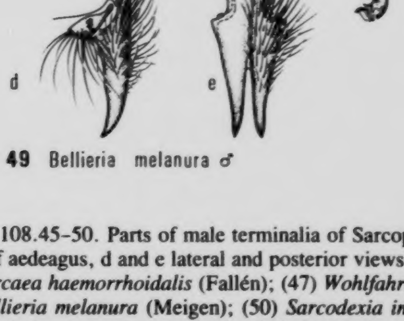
46 Bercaea haemorrhoidalis ♂



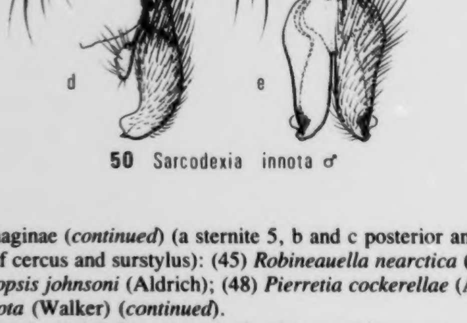
47 Wohlfahrtiopsis johnsoni ♂



48 Pierretia cockerellae ♂



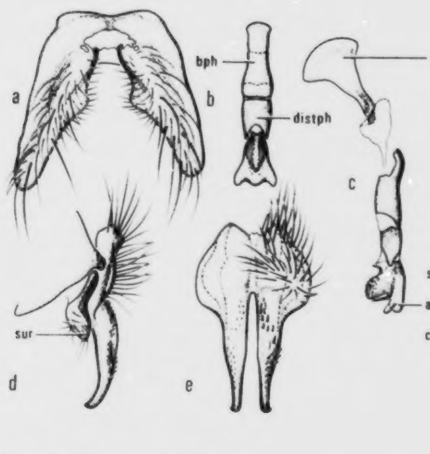
49 Bellieria melanura ♂



50 Sarcodexia innota ♂

Figs. 108.45–50. Parts of male terminalia of Sarcophaginae (*continued*) (a sternite 5, b and c posterior and lateral views of aedeagus, d and e lateral and posterior views of cercus and surstylus): (45) ***Robineauella nearctica*** (Parker); (46) ***Bercaea haemorrhoidalis*** (Fallén); (47) ***Wohlfahrtiopsis johnsoni*** (Aldrich); (48) ***Pierretia cockerellae*** (Aldrich); (49) ***Bellieria melanura*** (Meigen); (50) ***Sarcodexia innota*** (Walker) (*continued*).

Abbreviations: acroph, acrophallus; bph, basiphallus; distph, distiphallus; ej apod, ejaculatory apodeme; sur, surstylus.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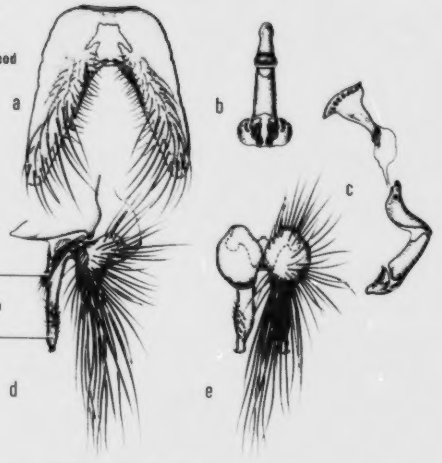
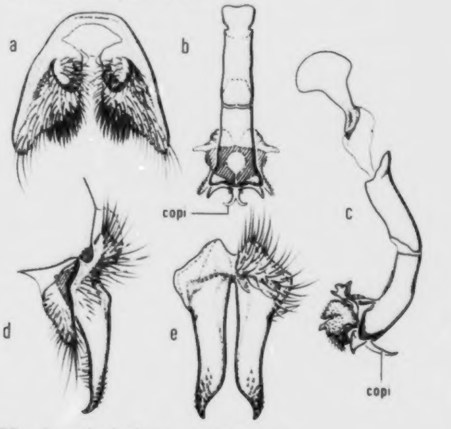
51 Blaesoxipha atlanis ♂



52 Protodexia hunteri ♂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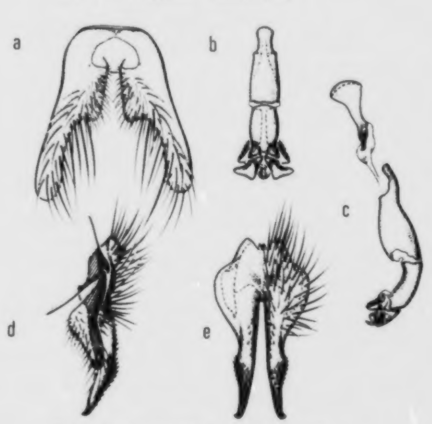
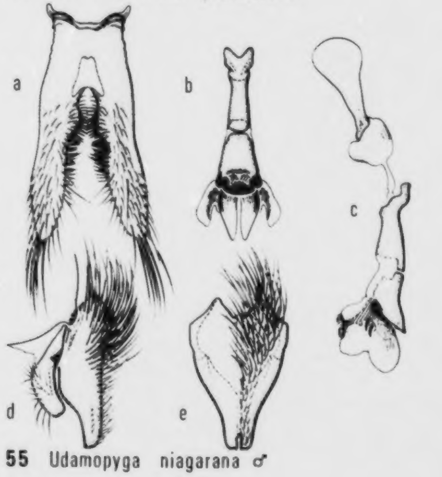
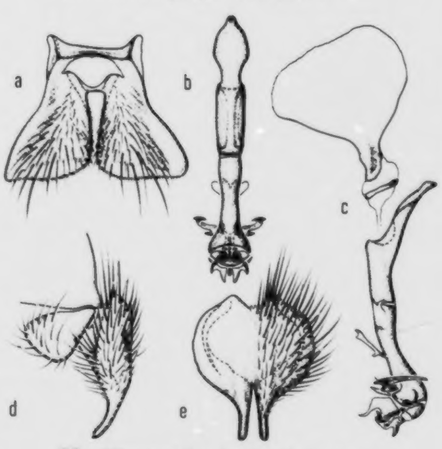
53 Acanthodotheca prohibita ♂



54 Acridiophaga aculeata ♂



55 Udamopyga niagarana ♂



56 Microcerella hypopygialis ♂

Figs. 108.51–56. Parts of male terminalia of Sarcophaginae (*continued*) (a sternite 5, b and c posterior and lateral views of aedeagus, d and e lateral and posterior views of cercus and surstylus): (51) ***Blaesoxipha atlanis*** (Aldrich); (52) ***Protodexia hunteri*** (Hough); (53) ***Acanthodotheca prohibita*** (Aldrich); (54) ***Acridiophaga aculeata*** (Aldrich); (55) ***Udamopyga niagarana*** (Parker); (56) ***Microcerella hypopygialis*** (Townsend) (*continued*).

Abbreviations: acroph, acrophallus; bph, basiphallus; cerc, cercus; distph, distiphallus; sur, surstylus.

34. Ctenidium absent. Four postsutural dorsocentral setae present. Female sternite 8 longer than broad with blunt-edged convex margin. Male terminalia as in Fig. 55 .... Tribal placement uncertain.... ***Udamopyga*** Hall

1 Nearctic sp., *niagarana* (Parker); widespread east of Rocky Mountains; Dodge 1965*a*

Ctenidium present in male. Usually three postsutural dorsocentral setae present, but if more, then sternite 8 of female broader than long with sharp-edged concave margin (Fig. 77) 35

35. Hind trochanter without spinules near base posteriorly .... PROTODEXIINI.... 36

Hind trochanter with two or three short curved spinules near base posteriorly (Fig. 26) .... IMPARIINI.... 45

36. Four postsutural dorsocentral setae present 37

Three postsutural dorsocentral setae present 38

37. At least three presutural acrostichal setae present, less than twice length of surrounding hairs. Crossvein dm-cu sinuate. Abdomen black in ground color (Fig. 77) .... ***Spirobolomyia*** Townsend

4 spp.; widespread east of Rocky Mountains; Lopes 1975

Presutural acrostichal setae absent. Crossvein dm-cu straight (Fig. 31). Abdomen partly reddish .... ***Fletcherimyia*** Townsend, in part

4 spp.; widespread east of Rocky Mountains

38. Presutural acrostichal setae absent. Crossvein dm-cu straight (Fig. 31) .... ***Fletcherimyia*** Townsend, in part

see couplet 37

Presutural acrostichal setae present. Crossvein dm-cu sinuate 39

39. R_1 setose .... ***Mantidophaga*** Townsend

3 spp.; central and southern U.S.A.; Lopes 1971*a*

R_1 bare 40

40. Tegula pale, or if dark, then terminalia black 41

Tegula dark. Terminalia red 44

41. Palpus black. Tegula pale. Male terminalia as in Fig. 51 .... ***Blaesoxipha*** Loew

1 sp., *atlanis* (Aldrich); widespread

Palpus yellow, or if black, then tegula also black 42

42. Male cerci with long brushes of straight hairs pointing downward (Fig. 52). Male mid femur with weak ctenidium (Fig. 35). Female tergite 5 closing slit-like, concealing tergite 6 and most of larvipositor; latter long, with haired lobes at base and rounded apex (Fig. 70) .... ***Protodexia*** Townsend

1 sp., *hunteri* (Hough); widespread

Male cerci short-haired. Female tergite 5 not closing slit-like; tergite 6 and larvipositor visible 43

43. Terminalia red. Larvipositor short and blunt (Fig. 72) .... PROTODEXIINI.... ***Opsophyto*** Townsend, in part

1 sp., *opifera* (Coquillett); widespread

Terminalia black. Larvipositor long and slender (Fig. 73) ..... ***Stenaulacotheca*** Townsend

2 spp.; widespread

44. Middle of propleuron bare. Female terminalia as in Fig. 71 .... ***Servaisia*** Robineau-Desvoidy

6 spp.; widespread

Middle of propleuron haired .... ***Amblycoryphenes*** Townsend

4 spp.; widespread east of Rocky Mountains

45. Middle of propleuron haired 46

Middle of propleuron bare 47

46. Aedeagus with copi (Fig. 53). Female sternite 7 longer than sternite 8, often elongate, slender, with subapical spines; sternite 8 short, transverse (Fig. 76) .... ***Acanthodotheca*** Townsend

18 spp.; mostly western and southwestern; Lopes and Downs 1951

Aedeagus without copi (Fig. 54). Female sternite 8 longer than sternite 7, usually elongate, tapered and bare (Fig. 78) .... ***Acridiophaga*** Townsend, in part
6 spp.; widespread

47. Tegula pale. Female terminalia as in Fig. 72. Small species, 5–7 mm long .... PROTODEXIINI .... ***Opsophyto*** Townsend, in part
see couplet 43

Tegula black 48

48. Four or five postsutural dorsocentral setae present, reduced in size anteriorly. Female terminalia as in Fig. 67 .... ***Kellymyia*** Townsend
5 spp.; widespread

Three postsutural dorsocentral setae present 49

49. Male cercus without spines or denticles, broadly subtriangular, shining. Female tergite 6 without marginal setae dorsally; tergite 8 well-developed, protruding hood-like over cerci (Fig. 68) .... ***Speciosia*** Roback
1 sp., *speciosa* (Lopes); Arizona, Louisiana, Mexico

Male cercus with clusters of spines or with scattered denticles (Fig. 54). Female tergite 6 with complete row of marginal setae; tergite 8 rudimentary; cerci exposed 50

50. Ocellar setae strong. Male cercus with scattered denticles (Fig. 54). Female sternite 8 long and tapering (Fig. 78) .... ***Acridiophaga*** Townsend, in part
see couplet 46

Ocellar setae weak. Male cercus and surstylus with several clusters of spines. Female sternite 8 short, transverse (Fig. 79) .... ***Abapa*** Dodge
1 sp., *deleta* (Wulp); Arizona, Texas, Mexico

51. Frontal rows of setae abruptly divergent at antennae, or if only gradually divergent, then with at least two setae below level of antennal base (Fig. 2) 52

Frontal rows of setae parallel, ending at antennal base. Rarely with a single seta below it (Fig. 3) 58

52. Costal spine present (Fig. 29). Male terminalia as in Fig. 56 .... MICROCERELLINI .... ***Microcerella*** Macquart
4 spp.; eastern and southern

Costal spine absent 53

53. Presutural acrostichal setae absent. Palpus yellow. Thorax with three postsutural dorsocentral setae .... NOTOCHAETINI .... ***Anolisimyia*** Dodge
1 sp., *blakeae* Dodge; North Carolina, Florida

Presutural acrostichal setae usually present and strong, but if absent or weak, then either palpus black or thorax with four postsutural dorsocentral setae ...... BOETTCHERIINI 54

54. Face extended well below vibrissae. Longest hairs of arista twice as long as width of first flagellomere (Fig. 14) .... ***Archimimus*** Reinhard
1 sp., *camatus* Reinhard; Arizona

Face not extended below level of vibrissae. Hairs of arista not longer than width of first flagellomere (Fig. 15) 55

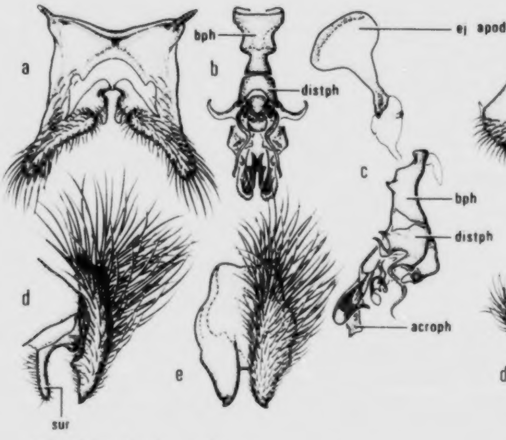
55. Parafacial pale golden or brownish. Usually a pair of weak presutural acrostichal setae present close to suture. Hind trochanter either with several spines posteriorly and dense spine-pad ventrally (male) (Fig. 27), or with spines or stiff short setae posteriorly (female). Male without outer vertical setae; male terminalia as in Fig. 57 .... ***Boettcheria*** Parker
5 spp.; widespread; Lopes 1950

Parafacial silvery white. No weak presutural acrostichal setae close to suture. Hind trochanter without spines. Male with strong outer vertical setae (Fig. 15) 56

56. Middle of propleuron bare. Male terminalia as in Fig. 58 ... ***Metoposarcophaga*** Townsend
4 spp.; widespread

Middle of propleuron haired 57

57. Presutural acrostichal setae as strong as dorsocentral setae. Ocellar setae about equal to upper frontal setae. Palpus black. Male without proclinate orbital setae .... ***Thelylepticocnema*** Townsend
6 spp.; western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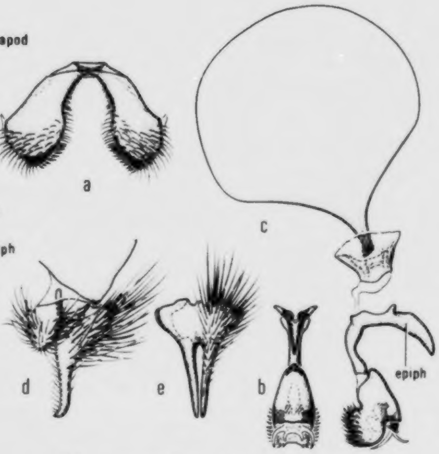
57 Boettcheria latisterna ♂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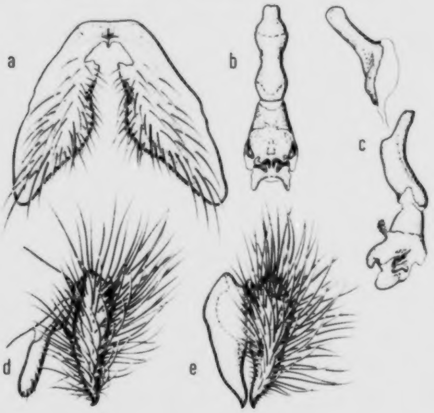
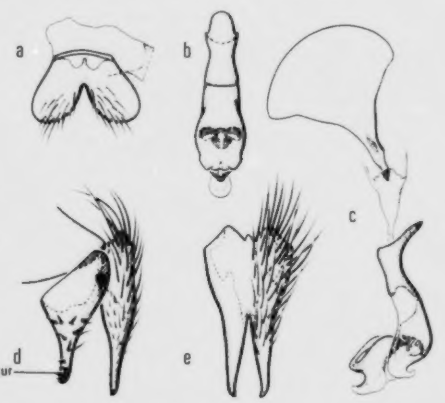
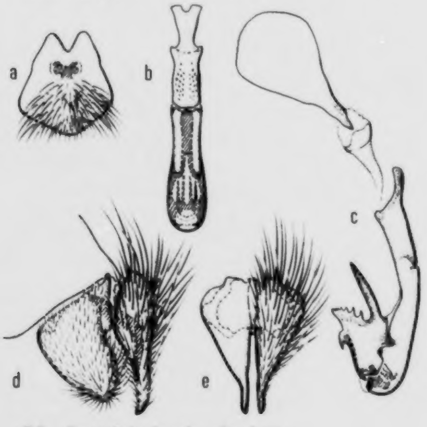
58 Metoposarcophaga importuna ♂



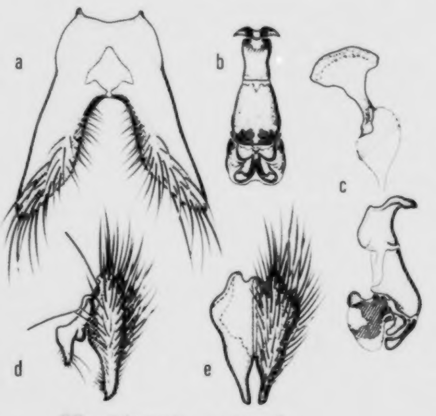
59 Neophyto setosa ♂



60 Sarcophagula occidua ♂



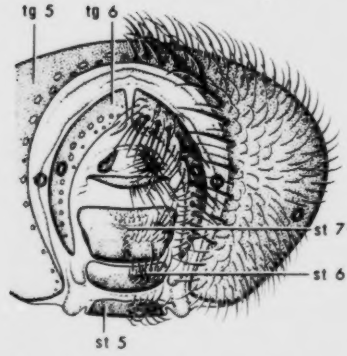
61 Sarcofahrtiopsis farri ♂



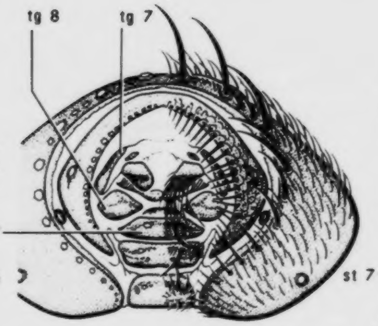
62 Johnsonia setosa ♂

Figs. 108.57–62. Parts of male terminalia of Sarcophaginae (*concluded*) (a sternite 5, b and c posterior and lateral views of aedeagus, d and e lateral and posterior views of cercus and surstylus): (57) *Boettcheria latisterna* Parker; (58) *Metoposarcophaga importuna* (Walker); (59) *Neophyto setosa* (Coquillett); (60) *Sarcophagula occidua* (Fabricius); (61) *Sarcofahrtiopsis farri* Dodge; (62) *Johnsonia setosa* Aldrich.

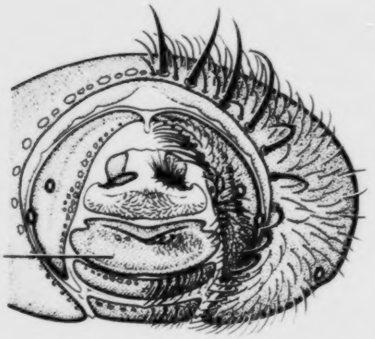
Abbreviations: acroph, acrophallus; bph, basiphallus; distph, distiphallus; ej apod, ejaculatory apodeme; epiph, epiphallus; sur, surstylus.


tg 5
tg 6
st 7
st 6
st 5

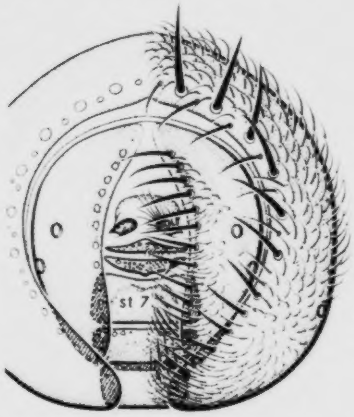
63 Arachnidomyia aldrichi ♀



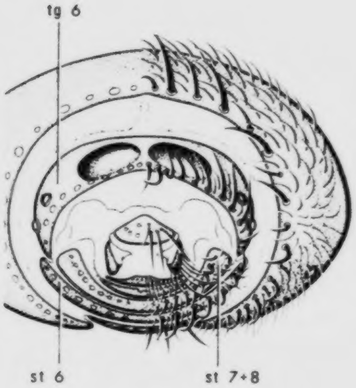
64 Liopygia crassipalpis ♀



65 Bercaea haemorrhoidalis ♀



66 Neobellieria bullata ♀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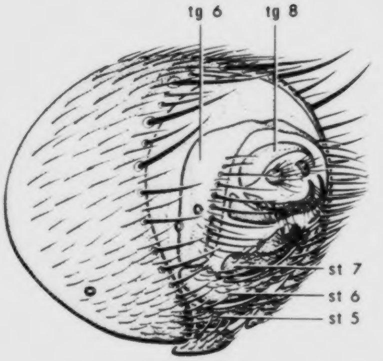
67 Kellymyia kellyi ♀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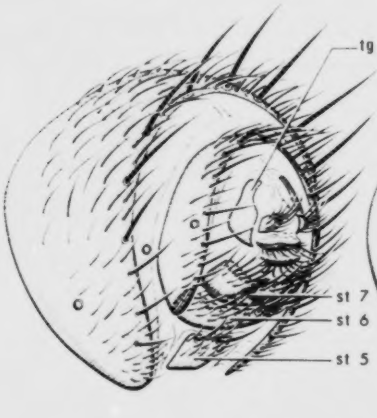
st 5

68 Speciosia speciosa ♀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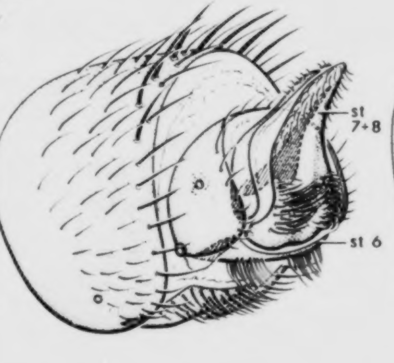
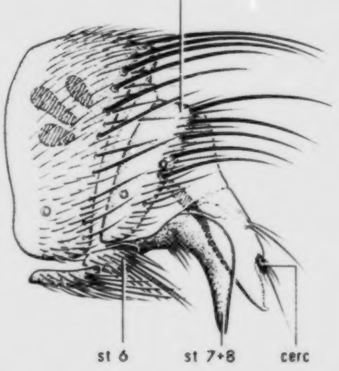
st 5

69 Sarcofahrtiopsis jamaicensis ♀



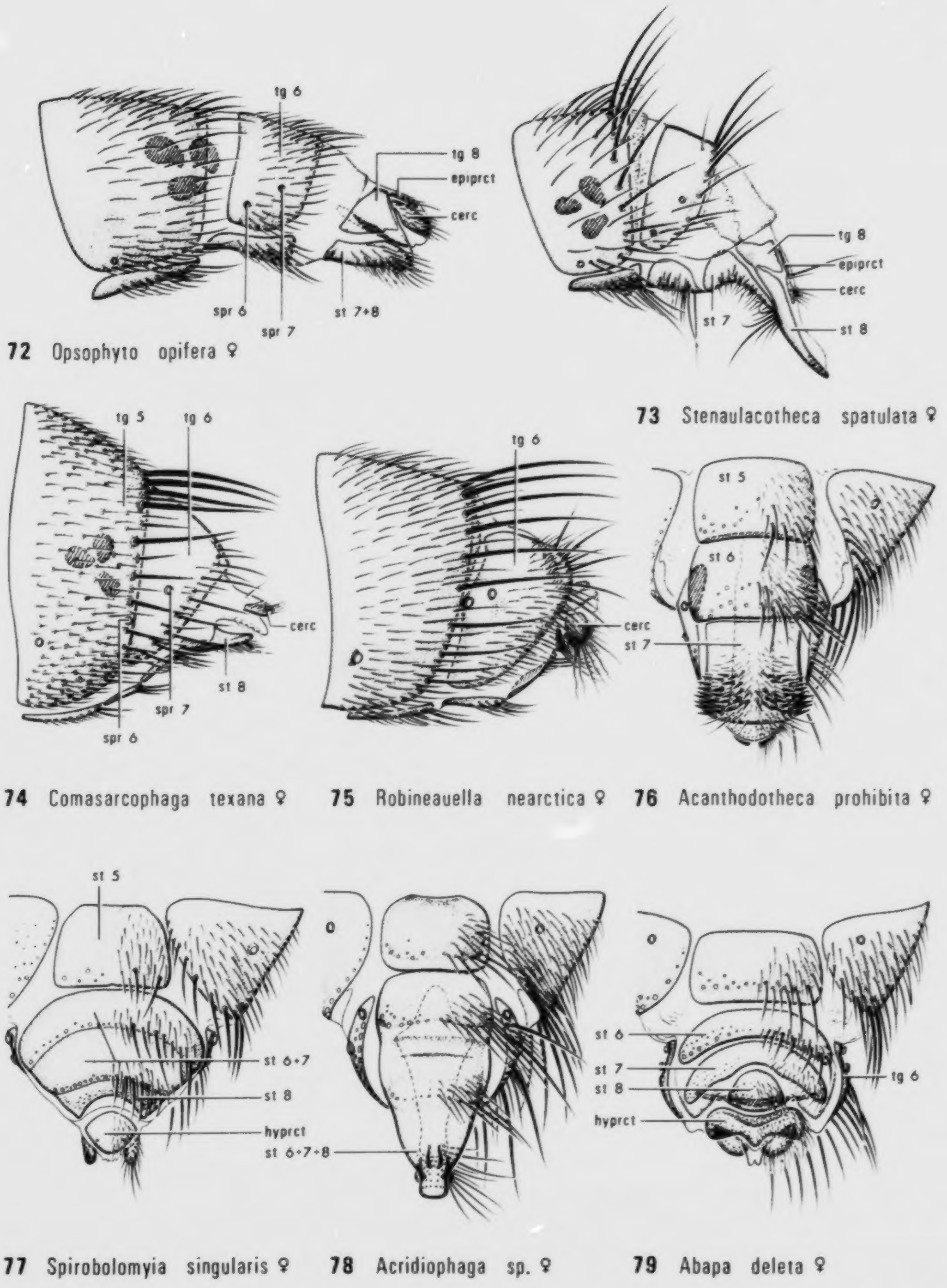
70 Protodexia hunteri ♀


tg 6
st 6
st 7+8
cerc

71 Servaisia sp. ♀

Figs. 108.63–71. Female terminalia of Sarcophaginae: posterior views of (63) *Arachnidomyia aldrichi* (Parker), (64) *Liopygia crassipalpis* (Macquart), (65) *Bercaea haemorrhoidalis* (Fallén), (66) *Neobellieria bullata* (Parker), and (67) *Kellymyia kellyi* (Aldrich); posterolateral view of (68) *Speciosia speciosa* (Lopes), (69) *Sarcofahrtiopsis jamaicensis* Dodge, and (70) *Protodexia hunteri* (Hough); (71) lateral view of *Servaisia* sp. (*continued*).

Abbreviations: cerc, cercus; st, sternite; tg, tergite.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cerc
st 7
st 5
st 6+7
st 8
hyprct
st 6+7+8
st 6
st 7
st 8
hyprct
tg 6

72 Opsophyto opifera ♀

73 Stenaulacotheca spatulata ♀

74 Comasarcophaga texana ♀

75 Robineauella nearctica ♀

76 Acanthodotheca prohibita ♀

77 Spirobolomyia singularis ♀

78 Acridiophaga sp. ♀

79 Abapa deleta ♀

Figs. 108.72–79. Female terminalia of Sarcophaginae (*concluded*): lateral views of (72) *Opsophyto opifera* (Coquillett), (73) *Stenaulacotheca spatulata* (Aldrich), (74) *Comasarcophaga texana* Hall, and (75) *Robineauella nearctica* (Parker); ventral views of (76) *Acanthodotheca prohibita* (Aldrich), (77) *Spirobolomyia singularis* (Aldrich), (78) *Acridiophaga* sp., and (79) *Abapa deleta* (Wulp).

Abbreviations: cerc, cercus; epiprct, epiproct; hyprct, hypoproct; spr, spiracle; st, sternite; tg, tergite.

Presutural acrostichal setae much weaker than dorsocentral setae. Ocellar setae hair-like. Palpus yellow. Male with a pair of proclinate orbital setae (Fig. 15) .... ***Erucophaga*** Reinhard
1 sp., *triloris* Reinhard; Arizona

58. Arista bare or short pubescent. Parafacial with conspicuous long hairs (Figs. 16, 17) .... NEOPHYTOINI 59

Arista plumose, its hairs at least as long as width of first flagellomere or, if shorter, then parafacial with inconspicuous short hairs 60

59. Arista bare; first flagellomere scarcely longer than wide. Parafacial with row of marginal setae. Vibrissal angle weak or absent (Fig. 16). Terminalia as in Fig. 59 .... ***Neophyto*** Townsend
4 spp.; south and central U.S.A.

Arista pubescent at base; first flagellomere twice as long as wide. Parafacial setae not in distinct row. Vibrissal angle developed (Fig. 17) .... ***Oppiopsis*** Townsend
1 sp., *sheldoni* (Coquillett); southern

60. Head length at vibrissa at least equal to head length at antennal base; vibrissal angle prominent; lower margin of head in profile straight (Figs. 18–20) ..... SAROTHROMYIINI 61

Head length at vibrissa shorter than at antennal base; vibrissal angle weak; lower margin of head rounded (Figs. 21, 22) .... JOHNSONIINI 63

61. R_1 setose. Female tergite 6 entire dorsally (Fig. 69). Male terminalia as in Fig. 61 .... ***Sarcofahrtiopsis*** Hall
2 spp.; Florida, Texas; Dodge 1965*b*

R_1 bare. Female tergite 6 divided by membrane dorsally 62

62. Parafacial narrow, with a single row of hairs above (Fig. 18). Male terminalia as in Fig. 60 .... ***Sarcophagula*** Wulp
2 spp.; Florida, Texas; Lopes 1956*a*

Parafacial broad, its hairs scattered (Fig. 19) .... ***Sarothromyia*** Brauer & Bergenstamm
possibly 2 spp.; southern and southeastern coastal

63. CuA_1 setose at base (Fig. 30). Frontal setae longest anteriorly (Fig. 21). Male terminalia as in Fig. 62 .... ***Johnsonia*** Coquillett
4 spp.; east of Rocky Mountains; Hallock 1938

CuA_1 bare. Frontal setae not longer anteriorly (Fig. 22) 64

64. R_1 bare. Three lateral scutellar setae present. Head as in Fig. 22 .... ***Camptops*** Aldrich
3 spp.; east of Rocky Mountains

R_1 setose. Two lateral scutellar setae present 65

65. Presutural acrostichal setae absent .... ***Sthenopyga*** Aldrich
3 spp.; southern and southeastern

Presutural acrostichal setae present .... ***Rafaelia*** Townsend
1 sp., *rufiventris* Townsend; Oklahoma, Texas

66. Meron (hypopleuron) with both hairs and setae (Fig. 23). Infrasquamal hairs present (Fig. 23). Tegula pale yellow to brown, concolorous with basicosta. Mid femur of male with apical posteroventral ctenidium (Fig. 99) .... PARAMACRONYCHIINI 67

Meron with row of setae only (Fig. 98). Infrasquamal hairs absent. Tegula usually black,[3] contrasting with pale basicosta. Mid femur of male without ctenidium .... MILTOGRAMMINI 73

67. Hind tibia with strong apical posterodorsal seta 68

Hind tibia without or with very weak posterodorsal seta 70

68. Frontal rows of setae abruptly divergent anteriorly (Fig. 80). Arista almost bare; first flagellomere dark brown to black. Palpus dark brown .... ***Brachicoma*** Rondani
4 spp.; widespread

Frontal rows of setae not abruptly divergent at anterior end (Fig. 81). Arista short pubescent; first flagellomere reddish. Palpus yellow 69

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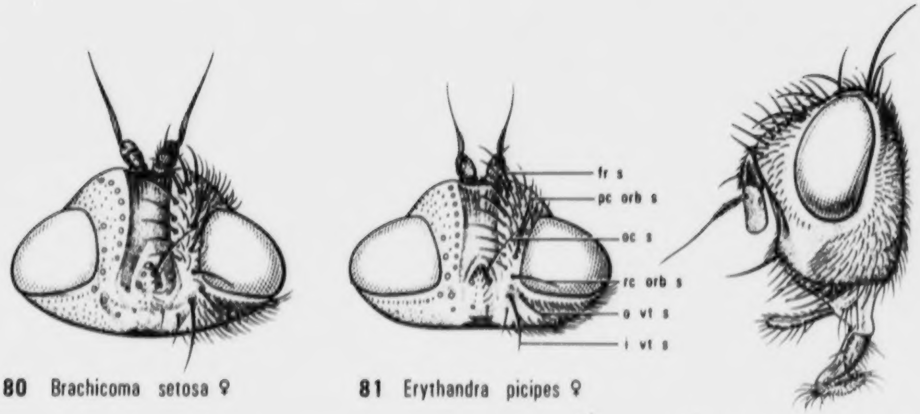
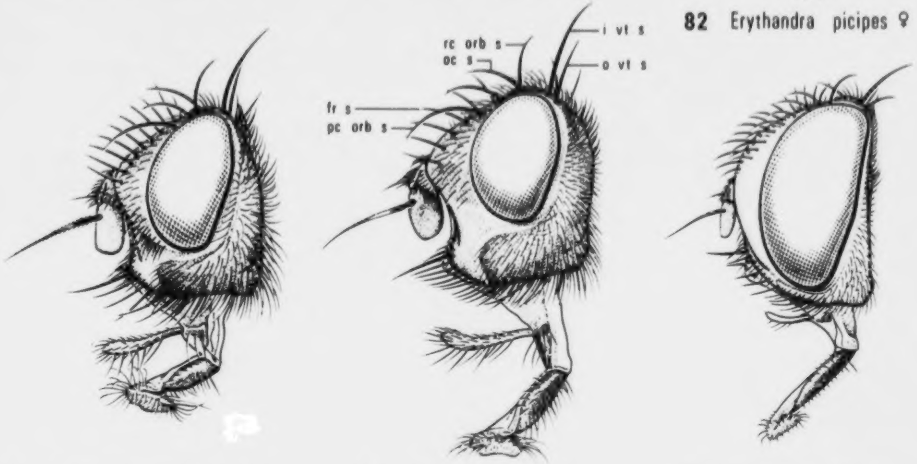
[3] Nearctic exceptions include *Hilarella* Rondani, *Taxigramma* Perris, and a few species of *Eumacronychia* Townsend.

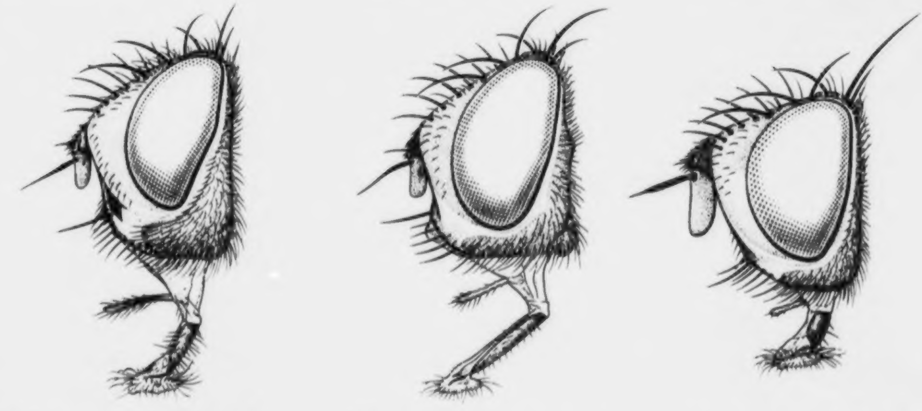


80 Brachicoma setosa ♀ **81** Erythandra picipes ♀

82 Erythandra picipes ♀



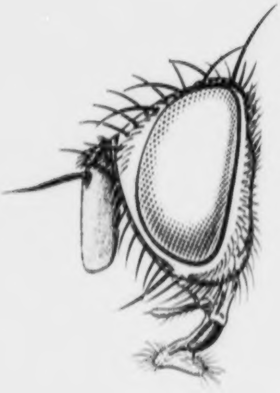
83 Toxonagria montanensis ♀ **84** Wohlfahrtia vigil ♀ **85** Amobia floridensis ♀



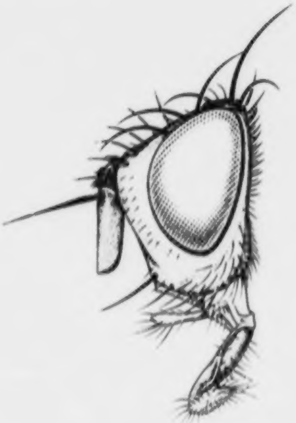
86 Macronychia aurata ♀ **87** Sphixapata trilineata ♀ **88** Oebalia aristalis ♀

Figs. 108.80–88. Heads of Miltogramminae: (80) dorsal view of *Brachicoma setosa* Coquillett; (81) dorsal and (82) lateral views of *Erythandra picipes* Brauer & Bergenstamm; lateral views of (83) *Toxonagria montanensis* (Parker), (84) *Wohlfahrtia vigil* (Walker), (85) *Amobia floridensis* (Townsend), (86) *Macronychia aurata* (Coquillett), (87) *Sphixapata trilineata* (Wulp), and (88) *Oebalia aristalis* (Coquillett) (*continued*).

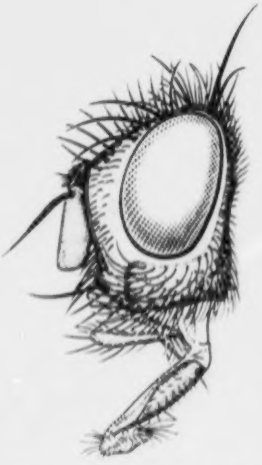
Abbreviations: fr s, frontal seta; i vt s, inner vertical seta; oc s, ocellar seta; o vt s, outer vertical seta; pc orb s, proclinate orbital seta; rc orb s, reclinate orbital seta.



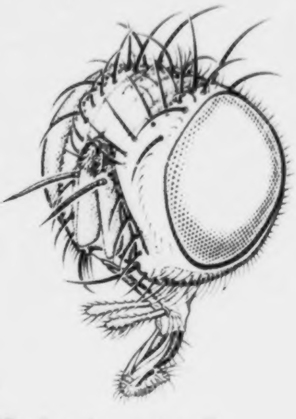
89 Ptychoneura woodi ♀



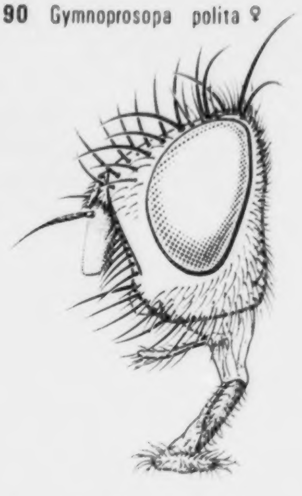
90 Gymnoprosopa polita ♀



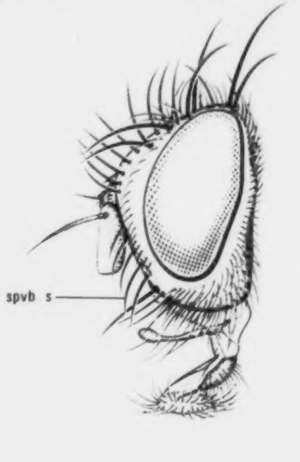
91 Gymnopsidia inflaticornis ♀



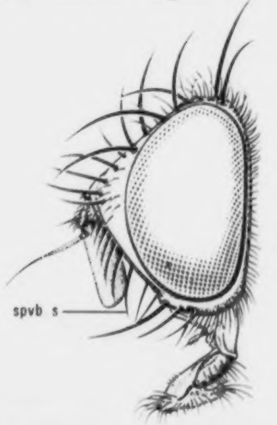
92 Euaraba tergata ♀



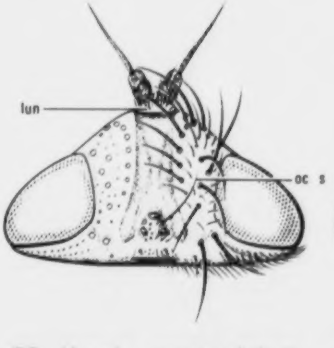
93 Arabiopsis cocklei ♀



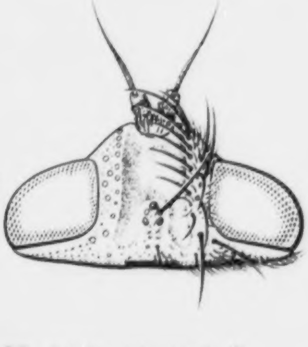
94 Sphenometopa nebulosa ♀



95 Allenanicia sinipalpis ♀



96 Metopia argyrocephala ♀



97 Anicia campestris ♀

Figs. 108.89–97. Heads of Miltogramminae (*concluded*): lateral views of (89) *Ptychoneura woodi* Shewell, (90) *Gymnoprosopa polita* Townsend, and (91) *Gymnopsidia inflaticornis* (Allen); (92) anterolateral view of *Euaraba tergata* (Coquillett); lateral views of (93) *Arabiopsis cocklei* Townsend, (94) *Sphenometopa nebulosa* (Coquillett), and (95) *Allenanicia sinipalpis* (Allen); dorsal views of (96) *Metopia argyrocephala* (Meigen) and (97) *Anicia campestris* (Fallén).

Abbreviations: lun, lunule; oc s, ocellar seta; spvb s, supravibrissal seta.

69. Head length at vibrissa less than at base of antenna (Fig. 82). Presutural acrostichal setae present. Hind femur of male normal .... ***Erythandra*** Brauer & Bergenstamm
2 spp.; widespread

Head length at vibrissa equal to that at base of antenna (Fig. 83). Presutural acrostichal setae absent. Hind femur of male thickened and arcuate (Fig. 102)...... ***Toxonagria*** Shewell
1 sp., *montanensis* (Parker); cordilleran

70. Presutural acrostichal setae present. Palpus black. Mid femur as in Fig. 99 .... ***Agria*** Robineau-Desvoidy
1 sp., *housei* Shewell; widespread temperate

Presutural acrostichal setae absent. Palpus yellow 71

71. First flagellomere slightly longer than pedicel. Parafacial bare on lower half (Fig. 84). Venter of abdomen subshining. .... ***Wohlfahrtia*** Brauer & Bergenstamm
2 spp.; 1 widespread, 1 western; James and Gassner 1947

First flagellomere nearly twice as long as pedicel. Parafacial haired to ventral margin of eye. Venter of abdomen dull, pruinose 72

72. Palpus distinctly clavate, almost bare above, sparsely haired below. Vibrissae short, not cruciate. Male frons about one-third of width of head. Length less than 7.0 mm .... ***Cattasoma*** Reinhard
2 spp.; southwestern

Palpus slender, thickly haired. Vibrissae normal, cruciate. Male frons about one-sixth of width of head. Length 7.0–12.0 mm .... ***Sarcofahrtia*** Parker
1 sp., *ravinia* Parker; widespread

73. Proepisternum distinctly tuberculate below. Two or more proepisternal setae present (Fig. 98) 74

Proepisternum not tuberculate. Only one proepisternal seta present or, if more, then either middle of propleuron haired, or R_1 setose 82

74. One pair of strong lateral scutellar setae present in addition to apical pair 75

Two pairs of strong lateral scutellar setae present in addition to apical pair 76

75. Cell r_{4+5} (apical cell) closed. Female abdominal tergite 6 entire .... ***Euphyto*** Townsend
3 spp.; widespread temperate

Cell r_{4+5} open. Female tergite 6 divided on middorsal line .... ***Euphytomima*** James
3 spp.; western

76. First flagellomere not more than three times length of pedicel 77

First flagellomere four to six times length of pedicel 80

77. Proclinate orbital setae absent, replaced by row of setulae (Fig. 85). Anterior margin of anepimeron (pteropleuron) with distinct swelling below ampulla (Fig. 98) .... ***Amobia*** Robineau-Desvoidy
6 spp.; widespread

Proclinate orbital setae present (Fig. 87). Anterior margin of anepimeron flat 78

78. Hind tibia with apical posterodorsal seta .... ***Senotainia*** Macquart
12 spp.; widespread

Hind tibia without apical posterodorsal seta 79

79. Mid tibia with two or three anterodorsal setae. Parafacial with moderately long hairs (Fig. 86) .... ***Macronychia*** Rondani
2 spp.; widespread

Mid tibia with a single anterodorsal seta near middle. Parafacial bare or with sparse very short hairs (Fig. 87).. ***Sphixapata*** Rondani
1 sp., *trilineata* (Wulp); widespread

80. First flagellomere orange. Hind tibia with apical posterodorsal seta .... ***Eusenotainia*** Townsend
1 sp., *rufiventris* (Coquillett); southern

First flagellomere black. Hind tibia without apical posterodorsal seta 81

81. Facial ridge with a few weak supravibrissal hairs (Fig. 88). Abdomen pruinose, with changeable pattern of dark median vitta and lateral spots. Terminalia as in Figs. 105 and 106 .... **Oebalia** Robineau-Desvoidy
1 sp., *aristalis* (Coquillett); widespread

Facial ridge with strong supravibrissal setae on lower two-thirds (Fig. 89). Abdomen shining black, with silvery segmental bands .... **Ptychoneura** Brauer & Bergenstamm
1 sp., *woodi* Shewell; eastern

82. Lunule bare 83

Lunule setose (Figs. 96, 97) 93

83. Cell r_{4+5} closed at wing margin. Lunule exposed 84

Cell r_{4+5} open. Lunule usually almost hidden 85

84. Last section of CuA_1 longer than preceding section (Fig. 103). Parafacial bare or nearly so. Proepisternal seta weaker than proepimeral .... **Taxigramma** Perris
1 sp., *heteroneura* (Meigen); widespread

Last section of CuA_1 shorter than preceding section (Fig. 104). Parafacial haired. Proepisternal and proepimeral setae subequal .... **Hilarella** Rondani
1 sp., *hilarella* (Zetterstedt); widespread

85. Facial ridge bare or with a few supravibrissal hairs below 86

Facial ridge with supravibrissal setae on more than lower half (Figs. 92–94) 91

86. Apical scutellar setae hair-like or absent .... **Eumacronychia** Townsend
20 spp.; most southwestern; Reinhard 1939*a*, 1965

Apical scutellar setae long and strong 87

87. Intermediate (second lateral) scutellar seta much longer than other two. Genal groove very large (Fig. 90). Crossvein dm-cu usually perpendicular to M .... **Gymnoprosopa** Townsend
6 spp.; widespread

Lateral and apical scutellar setae subequal. Genal groove small (Fig. 91). Crossvein dm-cu oblique to M 88

88. Three or four proclinate orbital setae present. Frons narrowed anteriorly. Gena with numerous long upcurved hairs (Fig. 91) .... **Gymnopsidia** Shewell
1 sp., *inflaticornis* (Allen); western

Two proclinate orbital setae present. Frons not narrowed anteriorly, or if so, then gena with inconspicuous fine hairs 89

89. Parafacial with inconspicuous fine hairs only. Abdominal segment 3 without median marginal setae .... **Opsidiotrophus** Reinhard
1 sp., *micidus* Reinhard; southwestern

Parafacial conspicuously haired and with row of setae near facial ridge. Abdominal segment 3 with a pair of median marginal setae 90

90. Middle of propleuron bare. Only one strong proepisternal seta present. R_1 setose. Abdomen shining black, with broad white segmental bands .... **Opsidiopsis** Townsend
1 sp., *oblata* Townsend; western

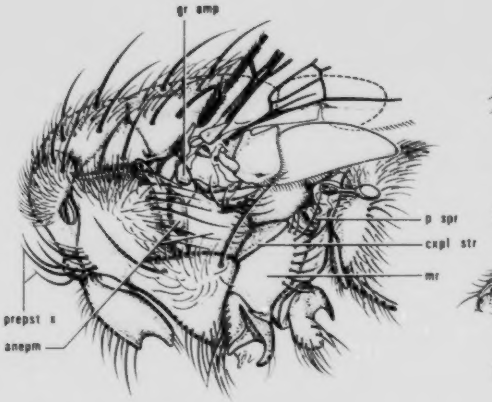
Middle of propleuron haired. At least two strong proepisternal setae present. R_1 bare. Abdomen yellowish gray pruinose, tessellate .... **Opsidia** Coquillett
1 sp., *gonioides* Coquillett; central and eastern

91. Apical scutellar setae absent. Arista thickened almost to apex (Fig. 92) .... **Euaraba** Townsend
1 sp., *tergata* (Coquillett); widespread

Apical scutellar setae strong. Arista thickened only on basal half 92

92. Face produced below vibrissa. Parafacial bare on lower half (Fig. 93). Abdominal segment 2 with median marginal setae .... **Arabiopsis** Townsend
1 sp., *cocklei* Townsend; western montane and boreal

Face not produced. Parafacial with a row of hairs on lower half (Fig. 94). Abdominal segment 2 without marginal setae .... **Sphenometopa** Townsend
3 spp.; southern


gr amp
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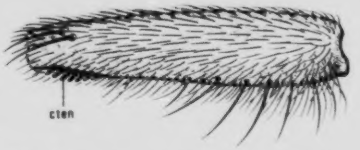
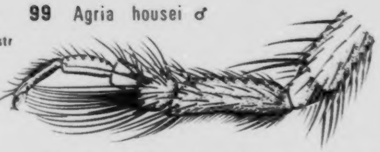
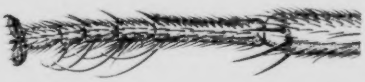
98 Amobia floridensis ♂



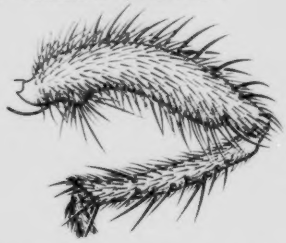
99 Agria housei ♂



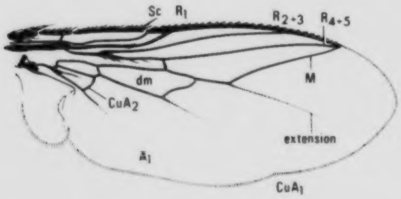
100 Phrosinella pilosifrons ♂



101 Anicia campestris ♂



102 Toxonagria montanensis ♂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R2+3 R4+5
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CuA2
extension
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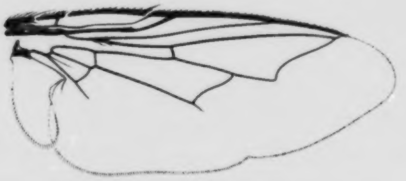
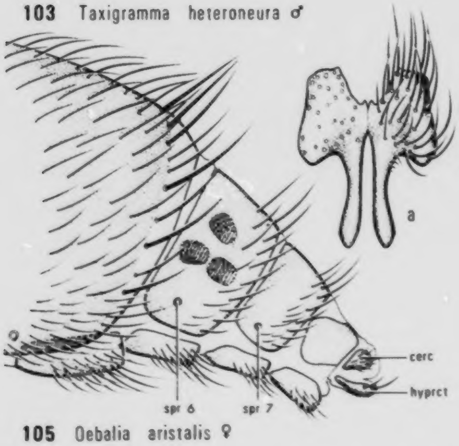
CuA1

103 Taxigramma heteroneura ♂



104 Hilarella hilarella ♂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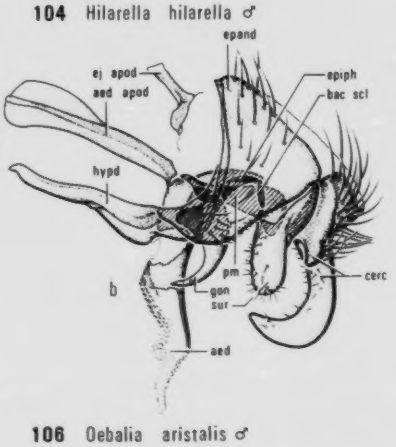
105 Oebalia aristalis ♀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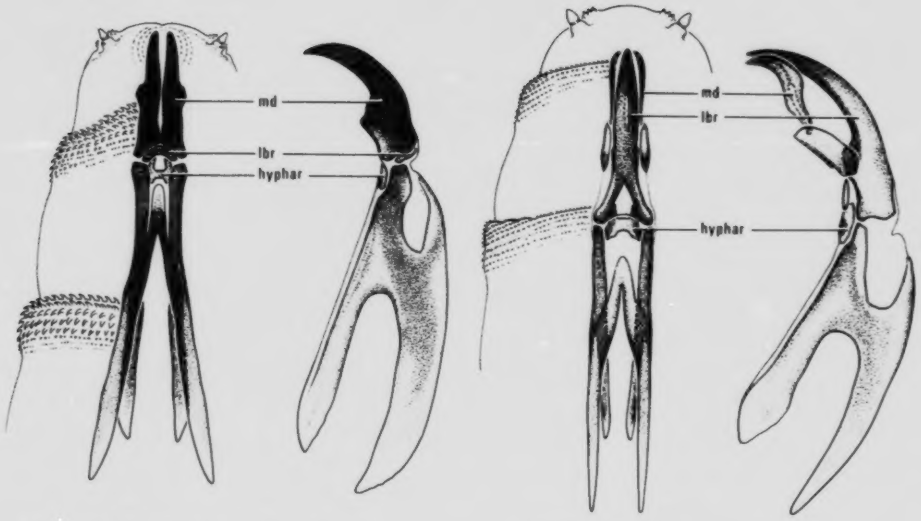
106 Oebalia aristalis ♂

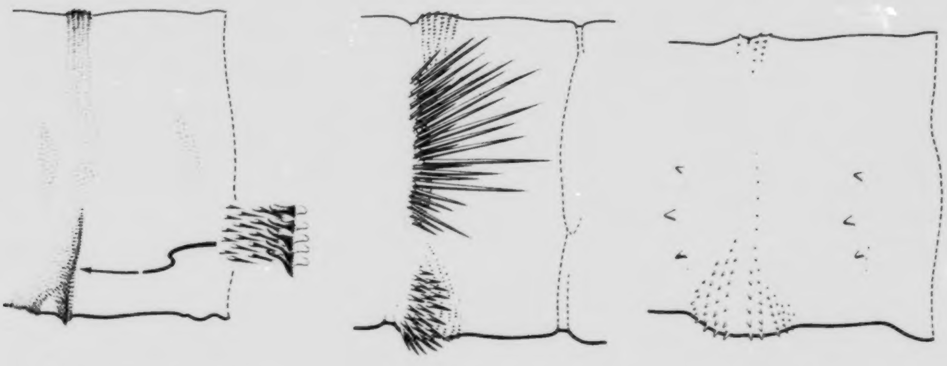
Figs. 108.98–106. Thorax, legs, wings, and terminalia of Miltogramminae: (98) lateral view of thorax of *Amobia floridensis* (Townsend); (99) posterior view of left mid femur of *Agria housei* Shewell; (100) posterior view of left fore tarsus of *Phrosinella pilosifrons* Allen; (101) dorsal view of left fore tarsus of *Anicia campestris* (Fallén); (102) anterior view of left hind femur and tibia of *Toxonagria montanensis* (Parker); wings of (103) *Taxigramma heteroneura* (Meigen) and (104) *Hilarella hilarella* (Zetterstedt); (105) lateral view of female terminalia of *Oebalia aristalis* (Coquillett); (106) posterior view of male cerci (a) and lateral view of male terminalia (b) of *Oebalia aristalis*.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; anepm, anepimeron (with swelling); bac scl, bacilliform sclerite; cerc, cercus; cten, ctenidium; cxpl str, coxopleural streak; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; gr amp, greater ampulla; hypd, hypandrium; hyprct, hypoproct; mr, meron; pm, paramere; prepst s, proepisternal seta; p spr, posterior spiracle; spr, spiracle; sur, surstylus.



107 Arachnidomyia aldrichi **108**

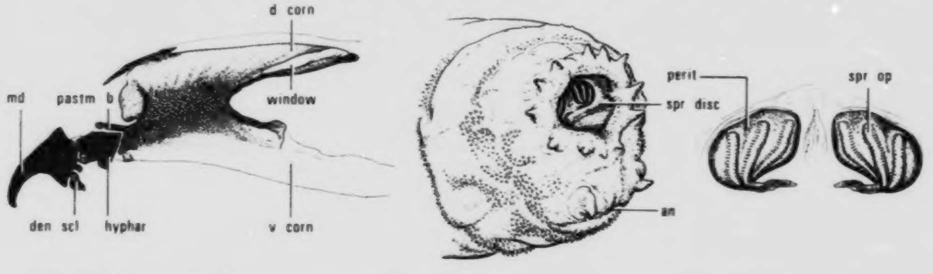
109 Sarcofahrtia ravinia **110**



111 Boettcheria cimbicis

112 Servaisia coloradensis

113 Brachicoma setosa



114 Ravinia querula

115 Ravinia querula

116 Ravinia querula

Figs. 108.107–116. Larvae of Sarcophagidae: dorsal and lateral views of cephalopharyngeal skeleton of first instar of (107, 108) *Arachnidomyia aldrichi* (Parker) and (109, 110) *Sarcofahrtia ravinia* Parker; left lateral views of second abdominal segment of first instar of (111) *Boettcheria cimbicis* (Townsend), (112) *Servaisia coloradensis* (Aldrich), and (113) *Brachicoma setosa* Coquillett; (114) lateral view of cephalopharyngeal skeleton, (115) oblique posterior view of last segment, and (116) posterior spiracles of third instar of *Ravinia querula* (Walker).

Abbreviations: an, anus; d corn, dorsal cornu; den scl, dental sclerite; hyphar, hypopharynx; lab scl, labial sclerite; lbr, labrum; md, mandible; pastm b, parastomal bar; perit, peritreme; spr disc, spiracular disc; spr op, spiracular opening; v corn, ventral cornu.

93. Parafacial with fine hairs or bare. Fore tarsus of male as in Fig. 100 .... ***Phrosinella*** Robineau-Desvoidy

5 spp.; widespread

Parafacial with a row of strong setae 94

94. Palpus rudimentary or absent (Fig. 95). Mid tibia without anterodorsal seta .... ***Allenanicia*** Townsend

4 spp.; widespread temperate; Sabrosky 1953

Palpus normal. Mid tibia with anterodorsal seta 95

95. Ocellar setae hair-like, weaker than reclinate orbital setae. Frontal rows of setae strongly divergent anteriorly, with a cluster of up-curved setae extending beyond base of first flagellomere (Fig. 96) .... ***Metopia*** Meigen

2 spp.; widespread

Ocellar setae as strong as reclinate orbital setae. Frontal rows not or little divergent, not extending beyond pedicel (Fig. 97). Fore tarsus of male as in Fig. 101 .... ***Anicia*** Robineau-Desvoidy

4 spp.; widespread

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RHINOPHORIDAE

109

D. M. Wood

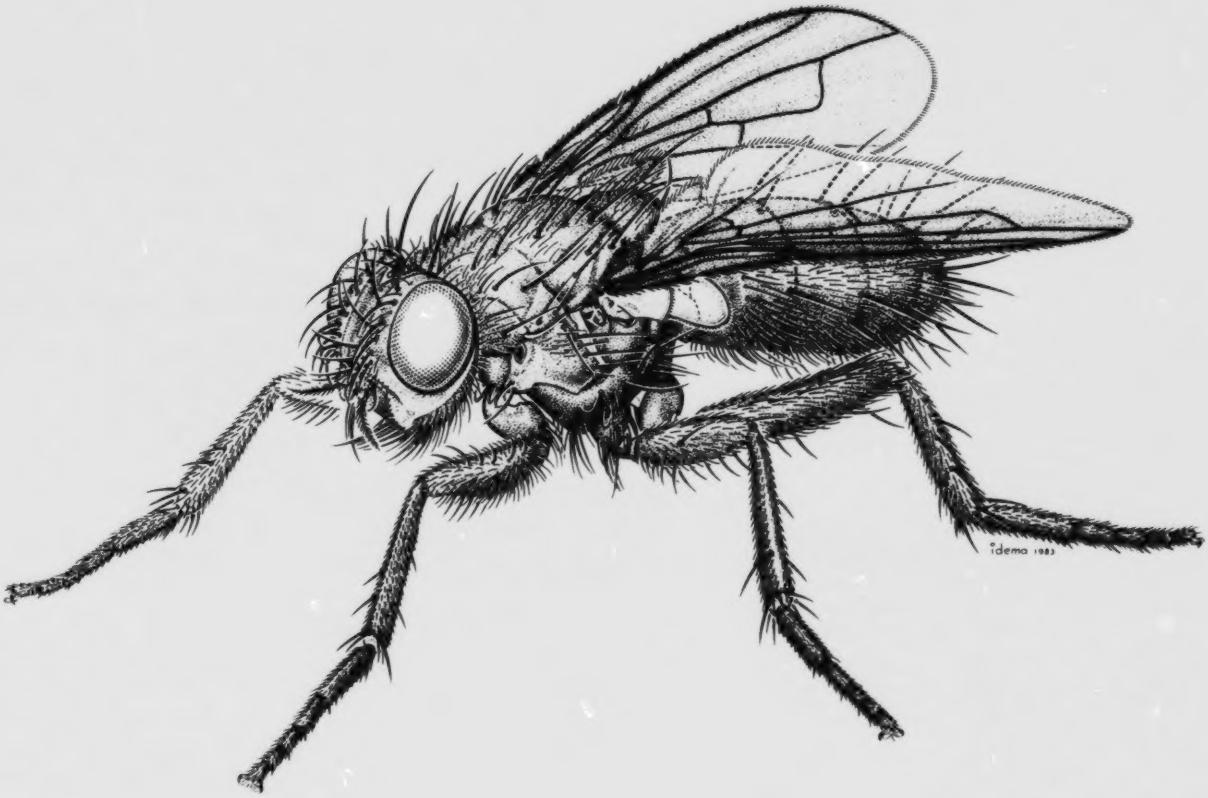


Fig. 109.1. Male of *Melanophora roralis* (Linnaeus).

Small to medium nondescript flies (Fig. 1), resembling sarcophagids; subscutellum weakly developed, intermediate in size between Sarcophagidae and Tachinidae; coxopleural streak present, usually distinct, evident as a membranous band between katepimeron and meron; abdominal sternites overlapped by adjacent tergal margins; lower calypter deflected laterally, away from body. Larva endoparasitic in woodlice (terrestrial Isopoda). Mandible of first instar subquadrate, with toothed anterior margin; cephalopharyngeal apparatus extremely long and slender.

Adult. Head: frons of male either dichoptic, as in female, with one to five (usually two) proclinate orbital bristles, or holoptic, usually without proclinate orbital bristles; one or two reclinate or lateroclinate upper orbital bristles present; anteriormost frontal bristle at level of scape. Antenna usually rather small, even in dichoptic males; arista usually plumose, but bare in *Phyto* Robineau-Desvoidy. Parafacial usually setose, either with a few small setae below lowest frontal bristle, or with a row of bristles sometimes increasing in length ventrally. Vibrissa well-developed; facial ridge with at most a few small setae above vibrissa; subvibrissal ridge with a row of bristles, distinctly separated ventrally from anterior margin of gena by extension of membrane of genal groove. Postcranium with stiff black hairs; postgena without longer pale setae.

Thorax: postpronotum with two or three bristles, but if with three, then these arranged in a straight line or triangle; proepisternum without patch of hair in middle; proepimeron usually with two major bristles, the lowermost smaller bristle arising close to ventral margin of proepisternum rather far below and behind the uppermost larger one, and sometimes (e.g. in *Melanophora* Meigen) directed anteriorly or anteroventrally; prosternum bare. Fringes (lappets) on either side of anterior thoracic spiracle small, scarcely occluding spiracle, almost absent in *Melanophora*. Scutal bristles reduced to minimum number in Calyptratae, not as numerous as in most Tachinidae; only one presutural acrostichal bristle (rarely none or two), one rather posteriorly placed postsutural acrostichal bristle (rarely two), two presutural and three postsutural dorsocentral bristles, only one presutural intra-alar (posthumeral) bristle, and usually two postsutural intra-alar bristles present; usually the anteriormost and posteriormost intra-alar bristles stout and the middle one slender, but less commonly the anteriormost slender and the middle and posterior ones stout; one presutural supra-alar (presutural) bristle usually present, sometimes with a small additional bristle anterior to it; two to four postsutural supra-alar bristles variable in size; first postsutural supra-alar (prealar) bristle either almost as large as the second and much closer to the transverse suture than to the second (*Phyto*), or smaller than and closer to the second (most genera), or absent (*Melanophora*, in which the apparent first is large but may be recognized as the second by its position). Notopleuron often with a small bristle or two between the two large bristles; katepisternum with two or three bristles. Meron with vertical row of bristles. Lappets of posterior thoracic spiracle poorly developed, reduced in most genera to tufts or fringes of hairs only partly covering spiracular opening (see Crosskey 1977, Figs. 41–44) best developed in *Phyto* (lappets similarly reduced in some genera of Tachinidae such as the tribe Lyphini). Scutellum with one to four pairs of marginal bristles, as follows: one pair of basal bristles (lacking in *Melanophora* or exceptionally long in *Tricogena* Rondani and *Microtarsina* Schiner); rarely (*Phyto* Robineau-Desvoidy) one additional small pair of bristles anterior to basal ones, as in ground plan of Calliphoridae; at least one pair of stout lateral bristles (lacking in *Tricogena* and *Microtarsina*); usually one pair of crossed apical bristles, arising close to each other. Subscutellum (Figs. 2, 3) weakly but distinctly developed, not as strongly convex on dorsal half as in Tachinidae (Fig. 2.66).

Wing with several small setae dorsally at base of R_{4+5} (*Phyto*, *Melanophora*) (Fig. 4), or with one or two larger ones (most genera), or bare (*Melanomya*, *Tricogena*). M either ending in wing margin, usually before wing apex, or in R_{4+5}, such that cell r_{4+5} (apical cell) is petiolate; petiole (i.e. veins M and R_{4+5}) sometimes very long, with M curving forward to meet R_{4+5} at right angles (Fig.4). Costal bristle long or short.

Fore tibia with one to three anterodorsal bristles and usually two posterior bristles; mid tibia with one or two anterodorsal bristles and two posterior bristles.

Abdomen: sternites 1–4 narrow, usually slightly overlapped by edges of tergites; sternite 5 with a simple U- or V-shaped cleft; edges of cleft not modified or thickened. Tergites 2–4 with only marginal bristles.

Male terminalia usually small relative to size of abdomen (Figs. 5, 7) and concealed within tergite 5; tergite 6 overlapped by tergite 5, sometimes nearly concealed; sternite 6 asymmetric, with left side larger and right side narrow and finger-like; spiracle 6 situated in membrane just anterior to syntergosternite 7 + 8; spiracle 7 situated within syntergosternite 7 + 8; the latter distinct from tergite 6, usually showing an indistinct transverse division. Epandrium (Figs. 7, 8) strongly arched dorsally; cerci rigid, usually deeply cleft or scarcely fused to each other medially, except fully fused in *Phyto;* surstylus short and broad or long and finger-like, or curved and much longer than cerci, and with a setose basal swelling in *Stevenia* Robineau-Desvoidy and *Tricogena;* bacilliform sclerite usually well-developed, articulated with surstylus, but free apically in *Melanophora* and minute and vestigial in *Morinia melanoptera* (Fallén). Hypandrium more or less fused with gonopod anteriorly; gonopod usually normal but flattened, supporting paramere posteriorly and aedeagus medially, and with a setose process in some genera; this process pointed and finger-like in *Stevenia*, minute in *Melanophora* and several other genera, or reduced to a group of setae in *Phyto;* paramere long, slender, and curved (*Stevenia*), or short and scoop-shaped with one stout seta on anterior surface near midlength; aedeagal apodeme usually as long as hypandrium; ejaculatory apodeme rather large to enormous (*Stevenia*, *Tricogena*); epiphallus rather broad, flattened dorsoventrally, and truncate apically (*Phyto*, *Melanophora*, *Rhinophora* Robineau-Desvoidy), or greatly reduced (*Melanomya*); dorsolateral process short and blunt (*Phyto*), long and slender (*Morinia* Robineau-Desvoidy), stout and blunt with membranous apex (*Stevenia*, *Tricogena*), or scarcely developed (*Melanophora*, *Rhinophora*); ventrolateral process usually scarcely developed.

Female terminalia (Fig. 6) (from Herting 1957) similar to that found in Calliphoridae, particularly in *Pollenia* (probably the plesiomorphic condition), but apparently always distinct from that in Tachinidae. Tergite 6 usually undivided dorsally, partially divided in *Stevenia atramentaria* (Meigen), more heavily chitinized and setose than subsequent tergites. Sternite 8 lacking median notch on posterior margin, either elongate as in *Anthracomyia melanoptera* (Meigen), or reduced to a small sclerite as in *Rhinophora* and *Stevenia*. Cerci and postgenital plate narrow and slender, presumably to permit the ovipositor to enter small holes and cracks.

Egg. Fusiform, white, with thin soft chorion; middorsal longitudinal band (possibly an aeropyle) sometimes surrounded with wing-like extension (Bedding 1973, Figs. 1–7); remainder of chorion either with longitudinal ridges (*Phyto*) or with hexagonal reticulations (remaining five British species, including *Melanophora*, described by Bedding 1973).

First instar. Antenna long, cylindrical or whip-like. Mandible subquadrate, with two or more curved teeth along anterior margin. Anterior portion of cephalopharyngeal apparatus long, slender, and parallel-sided when viewed in profile.

According to Bedding (1973), two types of first instars are distinguishable. In one group (which includes *Phyto*, *Melanophora*, and *Paykullia* Robineau-Desvoidy), the body is fusiform and covered with weakly sclerotized tubercles; the mandible has several lobe-like teeth anteriorly; the cephalopharyngeal apparatus has a deep narrow cleft anteriorly when viewed in profile; and the posterior end of the larva is modified for supporting the body in an erect position. In the other group (which includes *Cirillia* Rondani, *Rhinophora*, *Stevenia*, and *Tricogena*), the body is slightly flattened dorsoventrally and covered with often heavily sclerotized scales; each body segment has an encircling row of tubercles that may serve as pseudopods; mandible with one large and one or two much smaller curved teeth anteriorly; anterior portion of cephalopharyngeal apparatus not cleft anteriorly.

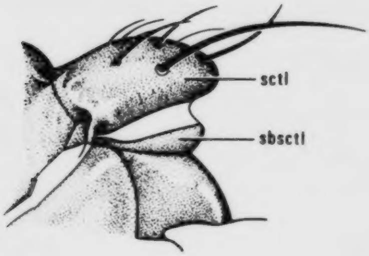
The above description was taken from Bedding (1973) and Thompson (1934). The first instar is known only for seven species, including the six British species described by Bedding. Later instars are inadequately known.

Biology and behavior. Life histories and immature stages of only nine species are known (Thompson 1934, Bedding 1973), and the following account is compiled from these two works. All species, as larvae, are obligate internal parasites of woodlice or sowbugs (Crustacea: Isopoda) and are apparently the only Diptera to parasitize this group (Crosskey 1977*b*). The eggs are not laid on the host, but on damp substrate where the host occurs. The egg when laid is unembryonated, the plesiomorphic condition found in most Calliphoridae, most Oestridae, and a few genera of Tachinidae. After several days larvae hatch, and the first instar must either wait for a passing woodlouse, or crawl about in search of it. Bedding has suggested that the pseudopodlike outgrowths on the first instar of *Rhinophora lepida* (Meigen), *Stevenia atramentaria* (Meigen), and *Tricogena rubricosa* (Meigen) (as the genus *Frauenfeldia* Egger) (and presumably also *Cirillia angustifrons* Rondani according to figures in Thompson 1934) enable the larva to wedge itself between the sternites of the host while attempting penetration. The specialized organ of attachment found in the other group of larvae may either aid the larva in gaining access to the host as it passes or may help it to penetrate the host. During its development, the posterior end of the larva remains enveloped by a sheath of host's hypodermis, called the integumental sheath or respiratory funnel. The tendency to stimulate the formation in the host of this sheath, or at least to use it to advantage for support and respiration, may be a synapomorphy of the Rhinophoridae and Tachinidae. Most of the larvae found by Thompson (1934) were supported in a respiratory funnel attached either to the integument surrounding the gills or along the pleural line near the host's posterior end. Overwintering takes place in the host, either as a first instar (*Rhinophora*) or a second instar (other genera). The puparium is formed within the empty skin of the host, usually with the anterior end directed toward the host's anterior end. Adults of *Melanophora roralis* (Linnaeus) appear in June in southern Canada; there are probably several generations each summer in the eastern United States. Males do not orientate to an aggregation site but fly from place to place, resting for a few seconds at a time on the sides of buildings or tree trunks.

Classification and distribution. The Rhinophoridae are a neglected group, and until recently the family has been variously divided between the Calliphoridae, Sarcophagidae, and Tachinidae. The most recent treatments of the group (Hennig 1973; Crosskey 1977*a*, 1977*b*) have argued for a separate family. Nevertheless, the limits of this family are by no means clear because the adults are quite variable and no character or group of characters has been found in the adult to render the group recognizable or to suggest that it is monophyletic. Inclusion in the Calliphoridae (Séguy 1941, Emden 1954) has been based mainly on shared ancestral characters (symplesiomorphy). Inclusion in the Tachinidae (Thompson 1934, Sabrosky and Arnaud 1965) could be argued on the shared occurrence of parasitism of arthropods, but this would render the resulting group indefinable morphologically on present knowledge.

Parasitism in woodlice may eventually prove to be a synapomorphy, but at present this feature is known for only eight species, all of European origin. The habit of depositing unembryonated eggs in the vicinity of the host, leaving the larva responsible for reaching its destination unaided, is unusual among calyptrates, being found elsewhere only in a few calliphorid genera, e.g. in *Pollenia* Robineau-Desvoidy and in the Cuterebrinae (Oestridae). Deposition of unembryonated eggs is surely the ancestral condition among calyptrates, for it is the characteristic mode of oviposition among Anthomyiidae, Muscidae, and most Calliphoridae. However, members of these groups usually oviposit directly on the larval substrate, not in its vicinity, and newly hatched larvae are presumably not adapted for locating the host on their own. Members of several groups of the Tachinidae deposit larvae to do their own searching (Dexiini and Tachininae, among others), but without exception these larvae are ready to hatch before the egg is deposited. Those few Tachinidae that deposit unembryonated eggs lay them directly on the host; this habit is presumed to be primitive (Herting 1963). Apparently all Sarcophagidae deposit larvae that have already hatched *in utero*. Deposition of eggs in the vicinity of the host, rather than directly on it, thus necessitating the first instar to find the host itself, may be a derived character. This, coupled with the habit of parasitism of woodlice, may eventually prove to be a synapomorphy that may show that the Rhinophoridae are a monophyletic group.

Crosskey's (1977*b*) review of the family included 23 genera in the world fauna. Only one of these, *Angioneura* Brauer & Bergenstamm (including synonyms *Opelousia* Townsend and *Opsodexiopsis* Townsend), has members indigenous to the Nearctic region. However, Shewell, in the preceding chapter dealing with the Calliphoridae, has included *Angioneura* in that family. The remaining 22 genera are restricted to the Old World, with the exception of the two species, mentioned in the key below, that have been introduced into the New World. The greatest diversity appears to be in the Mediterranean region (Herting 1961) and in Africa (Crosskey 1977*b*). Only four species have been recorded from the Oriental region (Crosskey 1977*a*).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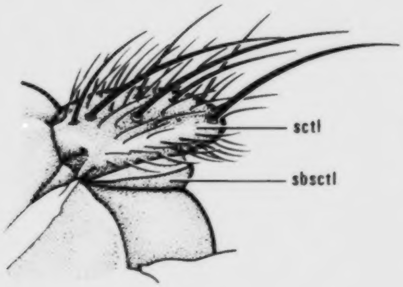
2 Melanophora roralis ♂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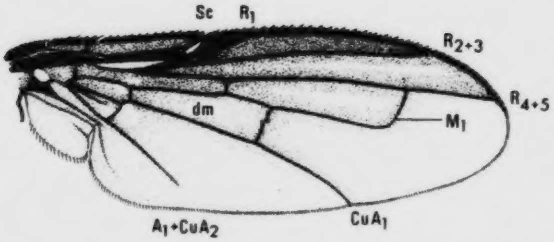
3 Phyto discrepans ♂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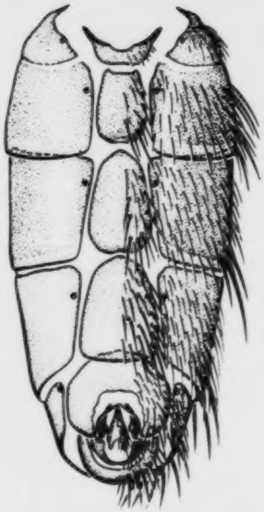
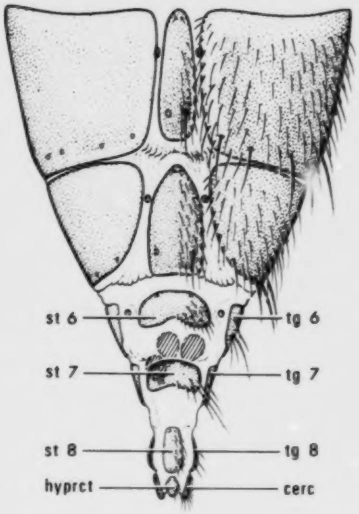
4 Melanophora roralis ♀



5 Melanophora roralis ♂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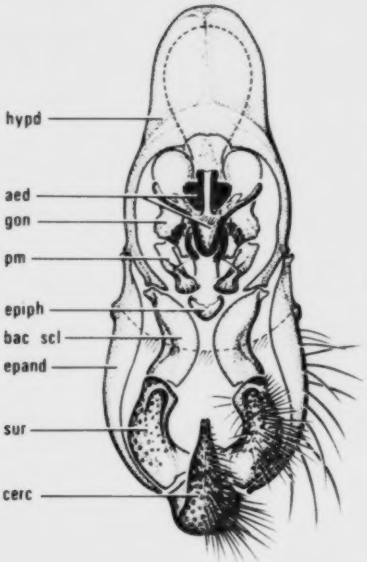
6 Melanophora roralis ♀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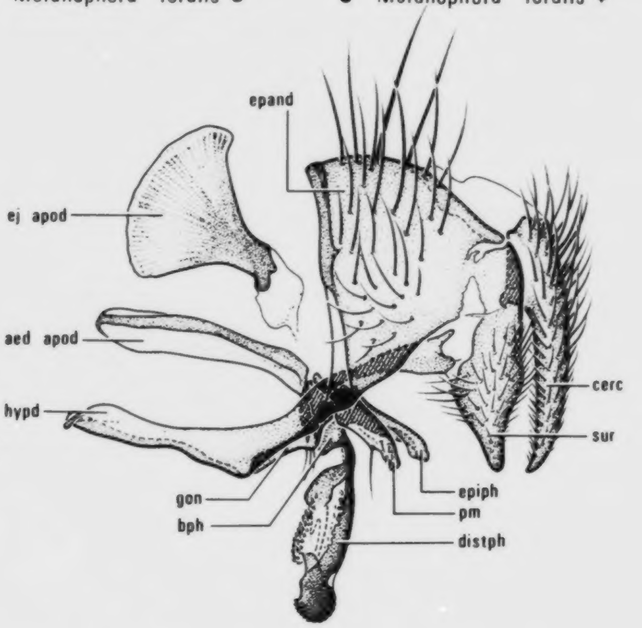
7 Phyto discrepans ♂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8 Phyto discrepans ♂

Key to genera

1. Wing entirely dark in male, or dark with a white apical spot in female (Fig. 4); M curving forward to meet R_{4+5} perpendicularly some distance from wing margin .... ***Melanophora*** Meigen

1 introduced sp., *roralis* (Linnaeus); eastern

Wing transparent; M angled forward obtusely to meet R_{4+5} close to wing margin; resulting combined vein shorter than crossvein r-m .... ***Phyto*** Robineau-Desvoidy

1 introduced sp., *discrepans* Pandellé; Newfoundland

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Figs. 109.2–8. Details of thorax, wing, and terminalia: lateral views of scutellum and subscutellum of (2) *Melanophora roralis* (Linnaeus) and (3) *Phyto discrepans* Pandellé; (4) wing of *Melanophora roralis;* (5) ventral view of male and (6) lateral view of female terminalia of *Melanophora roralis;* (7) ventral view and (8) lateral view of male terminalia of *Phyto discrepans.*

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; bac scl, bacilliform sclerite; bph, basiphallus; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; epiph, epiphallus; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; pm, paramere; sbsctl, subscutellum; sctl, scutellum; st, sternite; sur, surstylus; tg, tergite.

TACHINIDAE

110

D. M. Wood

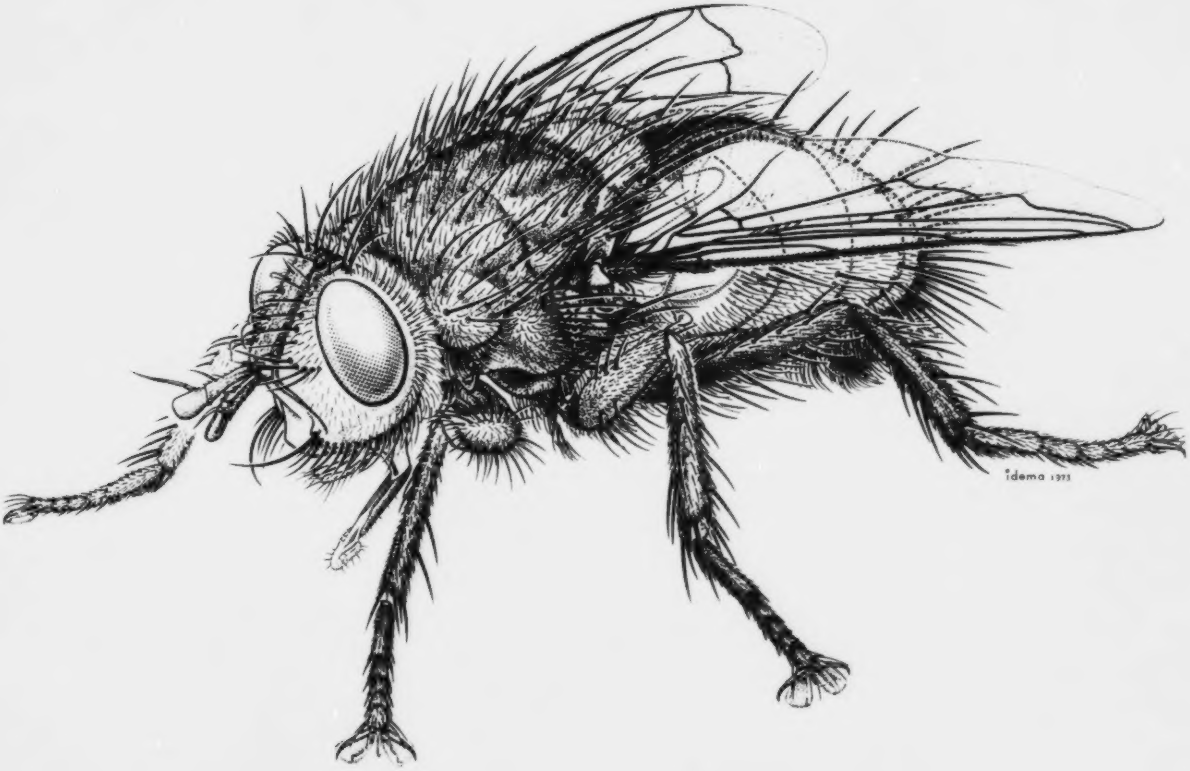

Fig. 110.1. Male of *Tachina florum* Walker.

Minute to very large flies (Fig. 1), often extensively bristled.[1] Subscutellum (postscutellum, infrascutellum) well-developed, as convex on upper half as on lower half when viewed in profile (Fig. 2.66, except *Bezzimyia* Townsend); meral bristles present (except in a few exotic species).

Larva endoparasitic in insects and occasionally in centipedes (there are unpublished records of parasitism of spiders and scorpions). First-instar larva with elongate hook-like or axe-shaped labrum broadly fused with cephalopharyngeal skeleton and extending from it as a continuation; mandibles (lateral plates) reduced or unrecognizable, without hooked apices. Second and third instars each with well-developed paired mandibles as in most calyptrates; posterior end of developing larva usually encased in a respiratory funnel formed from the host's hypodermis.

Adult. Head: extremely variable in proportions, usually higher than long with sloping frons, small face, and short antennae in holoptic males (Figs. 80, 84), or subquadrate in profile with more horizontal frons, long antennae, and face nearly as high as back of head (Figs. 89, 100). Frons of holoptic males moderately to very narrow, usually without proclinate lower orbital bristles; frons of dichoptic males and of females usually broad (narrow in some female Phasiinae), almost always with two pairs of proclinate lower orbital bristles, but rarely with one pair (Fig. 45) or more than two pairs (Fig. 52); frontal bristles usually medioclinate, extending forward only to level of pedicel in most Phasiinae and most Dexiinae (Figs. 55–58), in others extending farther forward with the row usually also curving laterally (Figs. 50–53) or rarely extending ventrally nearly to lower level of eye; fronto-orbital plate sometimes with one or more extra rows of frontal bristles flanking main row, especially among Goniini (Figs. 21 and 25, o fr s); one or two upper orbital bristles usually present, sometimes more, usually reclinate, sometimes lateroclinate, sometimes in line with uppermost frontal seta but usually arising lateral to it, rarely forming row well outside frontal row (Fig. 24). Ocellar tubercle usually distinct, although seldom prominent; ocelli rarely absent (Fig. 60); ocellar setae usually present, normally proclinate, rarely lateroclinate or reclinate (Figs. 2–4, 20, 21, 108), arising behind anterior ocellus except in *Euhalidaya* Walton (Fig. 52).

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[1] In this chapter, the term seta is used for all macrotrichia without reference to their size. Setae that are slender and usually rather straight are called hairs; bristles are large, stout, usually curved setae. The two are often intermingled.

Antenna extremely small (Figs. 80–82) to nearly as long as height of head (Figs. 98, 100), usually short in holoptic males, longer in dichoptic males; antennal bases usually contiguous (Fig. 87), occasionally separated (Figs. 84, 86). Scape usually inconspicuous. Pedicel with patch of short setae on anterior surface, one or two of which are elongate; in Dexiini pedicellar seta usually more than half as long as arista (Figs. 64, 83, 84), and usually with a patch of minute setae on medial surface intersecting with setae on opposite pedicel (absent in those species with separated antennae). First flagellomere usually subrectangular in profile with rounded or truncate apex, occasionally kidney-shaped in some Tachininae (Figs. 63, 130), rarely subdivided, bifurcate, or trifurcate (Fig. 2.45). Arista usually bare (except for microscopic pubescence), sometimes plumose (most Dexiini, Fig. 64), usually tapering evenly to thread-like apex, though often thickened partway up or nearly at apex (Figs. 128, 136); first and second aristomeres usually short and inconspicuous, although either or both sometimes elongate (Figs. 129, 132).

Parafacial (used in this chapter to refer to that part of head between ptilinal suture anteriorly and eye posteriorly, and between lowest frontal bristle dorsally and genal groove ventrally) usually pruinose, rarely shiny black or with shiny black areas around setae (Figs. 68–70), usually bare, although sometimes with setae (as hairs or bristles, or both) on any part thereof (Figs. 89–97). Face usually concave or flat and therefore not visible in profile, but sometimes convex and visible in profile, especially in most Tachinini, Aphriini, and Leskiini (Figs. 101, 102), or with median longitudinal carina as in some Dexiini and Phasiinae (Figs. 83, 84, 122). Lower corner of face (vibrissal angle) usually with an exceptionally large bristle, the vibrissa; lower facial margin (epistoma) usually level with vibrissa, but sometimes below level of vibrissa (Figs. 141, 145, 149); ridge below vibrissa usually with bristles (subvibrissal bristles), either separated from genal bristles by an extension of the genal groove (Fig. 142) or contiguous (Figs. 140, 141, 144); subvibrissal bristles numerous (Fig. 40), few (Figs. 41–43), or absent (Figs. 46, 145). Gena continuous with setose part of postgena, and more or less covered with setae, a few of which are bristle-like; dorsal border of genal hair patch sinuous, thus forming a genal dilation (Figs. 13, 40, 49), or concave or straight in which case genal dilation absent (Figs. 38, 39); anteroventral margin of gena usually with row of subgenal bristles extending posteroventrally or posteriorly along lower edge of gena; subgenal and subvibrissal bristles usually appearing to form a continuous row extending posteroventrally or posteriorly along lower edge of gena, often interrupted by a membranous extension of genal groove. Eye with fine straight hairs arising between facets; hairs sometimes so short as to be scarcely visible, with eye then appearing bare (Figs. 3, 4), or long and dense except along hind margin (Figs. 5–12); eye facets uniform in size, or if enlarged dorsally, then not changing in size abruptly even in holoptic males. Postcranium covered with short black setae or long pale hairs, or a mixture of both; postocular setae usually alternating long and short; median occipital area dorsal to occipital foramen usually flat, rarely deeply concave (*Opesia* Robineau-Desvoidy, Fig. 61).

Mouthparts always present, probably always functional, though occasionally very small (Figs. 80, 81). Clypeus usually inverted U-shaped or horseshoe-shaped, sometimes rectangular. Palpus usually clavate, exceptionally long in some Tachininae (*Adejeania* Townsend, Fig. 145), reduced in length in a few genera (Figs. 96, 97, 101), absent altogether in some species (Fig. 111). Prementum sometimes extremely long, probably to facilitate flower-feeding, in which case labella always minute (Figs. 110–115); or slender and elongate (*Siphona* Meigen, Fig. 143).

Thorax: postpronotum with two to five major bristles, but typically with four, namely three basal bristles (outer, middle, and inner) and one anterior bristle; basal bristles either arranged in a fairly straight line parallel to hind margin of postpronotum (Figs. 158, 160), or in a triangle with middle basal bristle displaced anteriorly to arise in front of outer basal bristle rather than between it and the inner basal bristle (Figs. 157, 159); anterior bristle situated anterolateral to inner basal bristle; occasionally also a fifth bristle present, namely an outer anterior one, anteromedial to displaced middle bristle and more or less in line with middle and outer basal bristles (Fig. 157); postpronotal bristles occasionally reduced to three or two (Figs. 156, 160, 161). Proepisternum usually bare, its central portion haired in some Tachininae and Blondeliini (Fig. 166), always with at least one anteroventrally directed proepisternal bristle at lower margin. Proepimeron usually with two or more bristles directed anterodorsally, rarely with lower seta inclined anteroventrally (Fig. 167). Prosternum bare (Fig. 155) or setose (Figs. 153, 154); setae confined to lateral margin, usually hair-like, but sometimes with one or more bristle-like; rarely one or two long straight bristles present without accompanying hairs (Fig. 154).

Scutum usually extensively bristled, especially in Goniinae, or with various bristles weakly developed, especially those in central part of scutum (Tachinini), or mostly absent (many Phasiinae); bristles arranged in four pairs of longitudinal rows (Fig. 2.65), namely a median acrostichal row, a dorsocentral row lateral to acrostichal row, an intra-alar row lateral to dorsocentral row, and a supra-alar row nearest lateral margin; each row is further subdivided by the transverse suture into a presutural and a postsutural portion; three presutural acrostichal bristles normally present, with posteriormost sometimes close to and sometimes more distant from suture; three postsutural acrostichal bristles also usually present; three presutural dorsocentral bristles usually present; three or four postsutural dorsocentral bristles present, the number usually constant within a species but often varying among closely related species; one to three presutural intra-alar bristles present, always one, sometimes with a smaller second one anterior to it close to edge of postpronotum (posthumeral), and sometimes with a third close to transverse suture; three postsutural intra-alar bristles usually present; two presutural supra-alar bristles present, with the anteriormost, close to postpronotum, displaced medially toward intra-alar row (therefore, in most literature, considered as one of the posthumerals) and with the posteriormost large, situated close to suture (in many works referred to simply as presutural); two to five postsutural supra-alar bristles present, but usually three; the anteriormost postsutural supra-alar (referred to as the prealar) always smaller than second postsutural supra-alar and usually also smaller than first postsutural dorsocentral in nearly all Tachinidae except in some Goniinae (Fig. 163) and a few Tachininae (Fig. 162), sometimes displaced anterolaterally (Fig. 162); in Exoristini a third small seta usually present between second and fourth (Fig. 164). Notopleuron typically with two bristles, occasionally with one or two additional smaller ones anterolateral to hindmost large bristle (Fig. 163); postalar callus usually with two large bristles and with up to three or more smaller setae between them; postalar wall (see Fig. 217) sometimes with a patch of hair. Scutellum usually with three or four pairs of marginal bristles, namely basal, lateral, subapical, and apical bristles, and one pair of discal bristles; basal bristles always present, usually directed somewhat dorsoposteriorly; typically only one pair of lateral bristles present, usually parallel (Figs. 182, 184), sometimes divergent (Fig. 185), sometimes with additional pairs (Figs. 188, 189), sometimes absent (Figs. 186, 190); subapical bristles divergent (Fig. 179), parallel (Fig. 180), or convergent (Fig. 182); apical bristles usually the smallest, often crossed or inclined dorsally and frequently reduced in size, hair-like, or absent (Fig. 182), less often large and crossed (Figs. 181, 183, 187, 190); lateral and subapical bristles occasionally replaced by a single large bristle intermediate in position (Fig. 183); typically one pair of discal bristles present, usually arising as far apart as subapical ones (Figs. 180, 184, 185) but sometimes closer together (Fig. 179), usually two-thirds distance from base but sometimes near apex as in Voriini (Fig. 187), in Tachinini present as a group of stout straight erect bristles. Subscutellum well-developed (except in *Bezzimyia*), usually evenly convex from top to bottom when viewed in profile (Fig. 2.66). Anepisternum (mesopleuron) sometimes with anterodorsal bristles, always with a posterior row anterior to pleural suture; katepisternum (sternopleuron) with one to four or more bristles, usually with three arranged in a triangle of various shapes (Figs. 173–175) or in a longitudinal row (Fig. 178), but if only one present (some Phasiini), then arising near posterodorsal corner of katepisternum (Fig. 171); anepimeron (pteropleuron) always with hair, usually with one or more short bristles, sometimes with an immense sickle-shaped bristle extending back beyond lower calypter (Figs. 215, 216); katepimeron (barette) usually bare, often with one to five hairs on anterior half, more extensively haired in Winthemiini (Fig. 170), or with a single bristle (*Phytomyptera* Rondani); meron (hypopleuron) always with a vertical row of bristles, rarely reduced to two or three in some Phasiinae (or none in the Neotropical phasiine genus *Tarassus* Aldrich).

Metepisternal area and metepimeron bare. Lappets (flaps) of posterior thoracic spiracle typically quite unequal; posterior lappet large, operculum-like; anterior lappet crescent-shaped (Fig. 170); some Tachininae with lappets more equal to each other, each extending across spiracular opening from anteroventral and posteroventral corners leaving a V-shaped opening (Fig. 169), sometimes with both lappets projecting outward (e.g. *Lypha* Robineau-Desvoidy, *Lydina* Robineau-Desvoidy).

Wing usually transparent, sometimes with distinctive spots or marks (Figs. 207–214), or entirely dark. M nearly always with a bend (cubitulus), found also in all Calliphoridae, Rhinophoridae, and Sarcophagidae, as well as in most Oestridae and some Muscinae; this bend acute (Figs. 193, 203), right-angled (most Exoristini, Fig. 197), or obtuse (Figs. 195, 199, 200); a short extension, or stub, sometimes evident beyond bend, in line with basal portion of M (Figs. 192, 202), sometimes called a stump vein (incorrectly called M$_2$); an apparent extension also sometimes evident, caused by a fold in membrane (Fig. 197); M usually ending in wing margin just behind apex of R$_{4+5}$, often ending in R$_{4+5}$ itself (Figs. 191, 192); cell r$_{4+5}$ (apical cell) then regarded, in most literature, to be closed and petiolate, occasionally ending in membrane at position of bend. Veins rarely crowded anteriorly (a few Voriini, Fig. 204). Base of R$_{4+5}$ with setae dorsally (except in *Cleonice* Robineau-Desvoidy) and usually also with setae ventrally; dorsal setae often extending along R$_{4+5}$ to crossvein r-m or even beyond; R$_1$ and CuA$_1$ also sometimes setose dorsally; Sc rarely setose ventrally (*Chaetoplagia* Coquillett, Fig. 205). Lower calypter (squama) usually well-developed, with its medial margin closely appressed against postalar wall, rarely (*Macquartia* Robineau-Desvoidy, some Phasiinae) deflected anterolaterally as in Rhinophoridae (Fig. 4.172), usually bare dorsally but with long erect hair in *Hystricia* Macquart (Fig. 215), exceptionally large in *Leucostoma* Meigen (Fig. 217).

Abdomen: slender, rarely narrowed basally (i.e. petiolate) to very broad (Figs. 240–245), convex dorsally or flattened to globose (forms laying microtype eggs), occasionally without bristles (Figs. 253, 254), but usually covered to varying degrees with stout spike-like erect bristles, occasionally emarginate apically (Fig. 240). Syntergite 1 + 2 with mid-dorsal concavity usually extending only partway back to hind margin (Figs. 236–238) but sometimes all the way to hind margin (Fig. 231); syntergite 1 + 2 usually without bristles, but sometimes with one pair of median marginal bristles (Fig. 231), rarely with more than one pair (Fig. 232); tergites 3 and 4 usually with at least one pair of median marginal bristles in female but with none in male of same species of some Goniinae, often with an additional transverse row of marginal bristles, and usually with one pair of median discal bristles, or sometimes with a transverse row or patch of discal bristles (some Tachininae) (Figs. 242, 243) or with a second pair in front of main pair (Fig. 239); tergite 5 normally with both median marginal and median discal bristles, although usually these somewhat irregularly arranged with scattered intermediate bristles. Sternite 1 wider than long, always fully exposed, usually abutting edges of syntergite 1 + 2, but separated by wide membrane in some Phasiinae (Fig. 254); sternites 2–5 usually overlapped by edges of adjacent tergites, often nearly concealed (Fig. 245), or abutting edges of tergites as in sternite 1 (some Tachinini, Fig. 244), in most Phasiinae separated from edges of tergites by membrane; each sternite usually with at least one pair of bristles or a transverse apical row; sternite 5 in male with U- or V-shaped apical cleft (Figs. 244, 245, 262); edges of cleft usually thickened or infolded and intimately fused at anterior (narrow) end of cleft with sternite 6 (Fig. 262).

Male terminalia usually retracted within tergite 5. Tergite 6 reduced, sometimes with a few bristles, often vestigial, represented only by setae, usually overlapped by tergite 5, though in many Tachininae fully exposed; sternite 6 well-developed on left side only, or with nearly symmetric development on right side as well, articulating with right side of syntergosternite 7 + 8; spiracle 6 situated in membrane. Syntergosternite 7 + 8 seldom showing distinct transverse subdivisions (distinct in *Macquartia*), occasionally with bristles (sometimes with two patches of bristles, indicative of fused origin), quite large and convex in Tachininae; spiracle 7 either appearing with spiracle 6 in membrane, or in syntergosternite 7 + 8. Epandrium usually smaller than syntergosternite 7 + 8. Cerci usually rigid, fleshy and pad-like only in *Cylindromyia* Meigen, usually closely approximated medially at base, separated apically to form an apical cleft, rarely (*Phebellia* Robineau-Desvoidy) with interlocking teeth (Fig. 263); cerci in Tachininae, Exoristini, Winthemiini, and some others without apical cleft, instead completely fused medially to form a hook (probably apomorphic). Surstylus usually well-developed, long and hook-like in *Cylindromyia* (i.e. perhaps replacing function of cerci), long and finger-like to short and rounded, closely applied to cerci in most groups, widely separated in Tachininae, or reduced to a plate with setose apical papilla in *Phorocera* Robineau-Desvoidy (i.e. evidently sensory rather than mechanical); bacilliform sclerite present, usually articulating with hypandrium and surstylus, not attached to surstylus in *Phorocera* (Wood 1972). Hypandrium usually Y-shaped, rarely (*Macquartia*, *Phorocera*) with the arms completely encircling base of aedeagus to meet each other behind it, forming a tube; gonopod (pregonite) with somewhat triangular base and finger-like or hook-like setose projection, fused along its anterior and lateral edges with medial margin of arm of hypandrium, or (in Dexiinae) strap-like, with a minute nonsetose projection or none at all, articulating at its anterior end with hypandrium (Fig. 261); paramere (postgonite) usually hook-like, paralleling epiphallus when latter present, or (in Dexiinae) located parallel to basiphallus and about same length and shape as this structure; basiphallus usually short (elongate in most Dexiinae); distiphallus usually lacking distinct dorsolateral or ventrolateral processes in Dexiinae hinged to anterior surface of basiphallus near apex, in Voriini very long, strap-like, and coiled, asymmetric in Phasiinae.

Female terminalia (from Herting 1957) usually with tergites 6 and 7 intact dorsally (probably the plesiomorphic condition); often tergite 7, and sometimes also tergite 6, interrupted middorsally, sometimes reduced to a pair of small sclerites on either side of sternite 7; spiracle 6 always located in lateral margin of tergite 6; spiracle 7 either located in tergite 7 (undoubtedly the primitive condition), or displaced anteriorly to sternite 6; sternites 6 and 7 usually broadened at the expense of adjacent tergite, broader than sternites 2–5; lateral corners of tergite 6 in some Phasiinae (*Leucostoma*, *Imitomyia* Townsend) produced posteriorly as a pair of clasping lobes (Fig. 249); sternite 7 in some Blondeliini and in *Phorocera* (Exoristini) modified into a hook-like piercer, grooved on its posterior surface to accommodate remainder of ovipositor (Figs. 248, 256, 257). Tergite 8 usually divided middorsally into two remnants; sternite 8 never subdivided or emarginate apically, often large and plate-like, in most Phasiinae elongated to form a piercer partially ensheathed in sternite 7 (Fig. 253) or reduced to a small lobe usually with sensory pores and setae probably for sensory contact with host; sternite 10 (postgenital plate) usually small, rounded, and weakly sclerotized, hidden above sternite 8, but in *Cylindromyia* (Phasiinae) modified into an elongate sharp piercer. Cerci small, pad-like, probably always sensory in function.

Egg. Primitively, as in oviparous species (Exoristini, Winthemiini, *Aplomya* Robineau-Desvoidy, some Blondeliini), white, oval or elliptic to nearly circular, convex and rather firm dorsally, membranous and flattened ventrally, with an adhesive coating to stick to host, or rarely (*Phorocera* subgenus *Pseudotachinomyia* Smith) cylindrical and adapted for partial insertion into host's integument (Wood 1972); anterior cleavage line evident in Exoristini and Winthemiini delineating an operculum through which larva hatches (Fig. 264); in the majority of other species, such a cleavage line absent (larva breaks through ventral chorion); one or two groups of aeropyles present dorsally. In ovolarviparous species, dorsal chorion less firm, transparent or white, with or without remnants of aeropyles; in the most derived state dorsal chorion hardly different from ventral surface except for lack of adhesive material. Egg in microovolarviparous Goniini minute and limpet-like, with tough often highly sculptured upper chorion (Figs. 266–268).

First-instar larva. Fundamentally different from later instars in cephalopharyngeal structure. Anterior end of cephalopharyngeal skeleton (probably the labrum although homology has not been established, usually called "mouth hook" in previous literature) extending forward as a hook-like or hatchet-like structure, often with serrated anterior margin, presumably to facilitate access to the host. Lateral plate (probably a reduced mandible, although homology not yet convincingly established) a vaguely defined sclerotized area on side of mouth opening, without hook-like extension and probably not functional as is mandible of other calyptrates.

Second- and third-instar larvae. Labrum minute. Mandibles present, symmetrical, articulated with hypopharynx which is in turn articulated with cephalopharyngeal skeleton (Figs. 5.31, 5.32). Anterior spiracle simple, with one or more papillate openings at apex (Figs. 5.22, 5.23), usually elevated from surface of prothorax, sometimes absent. Posterior spiracle usually heavily sclerotized, flush with abdominal surface or elevated on a cone-like prominence (Figs. 5.21, 5.27), never concealed in a depression as in Sarcophagidae; each spiracle with usually three, sometimes four or more, rows of openings; rows straight (Fig. 5.25) or sinuous (Fig. 5.27), branched, or subdivided into "segments" or areas (Figs. 5.21, 5.30) (see also couplet 62, Ch. 5).

Biology and behavior. The life cycles of a wide range of genera of Tachinidae are now known. All known larvae are parasitic on other arthropods, almost exclusively on other insects. Although many species have not yet been reared, so many have been shown to be parasitic that this feature is probably characteristic of the family as a whole.

The most primitive mode of attack on an exposed host is to attach an undeveloped egg (Fig. 264) onto the skin of the host. The large oval planoconvex egg is translucent at the moment of oviposition but turns white on drying and is quite conspicuous. Its flat ventral surface is covered with a sticky substance that ensures firm adhesion to any part of the host. The developing embryo within respires via many minute pores called aeropyles, grouped at each end of the egg. When ready to hatch, the larva either pushes off the cap, or operculum, at the anterior end of the egg and burrows into the host in front of it, or burrows directly into the host through the floor of the egg. The species that deposit this type of egg lack a uterus, or ovisac, for retention of eggs undergoing embryonic development. Hence such eggs show little or no embryonic development and are said to be unembryonated. Eggs left to undergo embryonic development on the skin of the host remain vulnerable for several days. During this period they may be eaten off by the host or may become lost when the host molts. Contrary to popular belief, this type of egg is characteristic of only a small number of genera, constituting a tiny fraction of the Tachinidae. These genera, believed to be among the most primitive members of the family (Herting 1960), comprise the Phasiinae, the goniine tribes Exoristini and Winthemiini, a few Blondeliini (*Meigenia* Robineau-Desvoidy, *Medina* Robineau-Desvoidy, *Belida* Robineau-Desvoidy), and *Aplomya* in the Eryciini.

Several modifications to this primitive system have evolved in certain genera, which serve to speed up entry of hatching larvae into the host and thus allow them to avoid the pitfalls described above. A small departure from simple deposition of the primitive planoconvex egg on the host's skin involves modifications of the female's abdominal sternites to facilitate partial or complete insertion of the egg into the body of the host. In the Exoristini, members of one genus, *Phorocera*, have developed devices for partly or entirely inserting their unembryonated egg into the skin of the host (Figs. 248, 265) (Herting 1963, Wood 1972). Although a few phasiines, e.g. *Gymnosoma* Meigen and *Trichopoda* Berthold, attach planoconvex eggs to the surfaces of their hemipteran hosts, some abdominal sternites of females of most Phasiinae have also developed into rather elaborate piercing structures for inserting their unembryonated eggs into their hosts (Figs. 253, 254).

Certain other strategies are used by some genera to allow them to parasitize hosts that are too aggressive, that are protected by spines, hairs, or webbing, or that are hidden and otherwise inaccessible to the adult fly. Probably the most important advance in reproductive strategy, shared by the vast majority of Tachinidae, is the storage of eggs in an ovisac until embryonic development is complete. The ovisac is little more than an enlargement and elongation of the common oviduct, with increased tracheal supply to provide more oxygen for the developing larvae. Thus a single female may carry hundreds or thousands of eggs, the ones farthest from the ovaries ready to hatch at the moment of deposition. Unlike members of the Sarcophagidae, which are all viviparous (i.e. in which eggs hatch within the female and active larvae are deposited directly on the substrate), all Tachinidae are apparently ovolarviparous (i.e. eggs hatch after they are deposited). Sometimes a female will die before her offspring do, and they may subsequently hatch and escape from her abdomen. Except for such instances, however, no egg shells have ever been encountered, after thousands of dissections, in the ovisac of any species. Eggs of many species, however, may hatch within seconds after deposition, giving the appearance of larvipary. The advantage of rapid hatching after oviposition is obvious; the larva is immediately able to begin penetrating the host. In spite of such efficiency, the system is not infallible. I observed one species of arctiid biting its own integument, in an apparently successful effort to destroy the larva of *Calolydella lathami* (Curran) before it was able to penetrate completely.

Most potential hosts escape direct attack from ovipositing tachinids by remaining inaccessible during the day while females are active; either the larvae hide in the litter or soil, or they are protected by webbing. Both can thus avoid the direct attack of adult flies by feeding at night.

A large group, the Goniini, has circumvented the problem of host inaccessibility by evolving a system in which minute eggs are produced for consumption by the host. Termed microtype eggs, they somehow escape being crushed by the host's mandibles, hatch in the foregut when stimulated by digestive enzymes, and burrow through the gut wall into the haemocoel. The fly need only find recently damaged foliage of the appropriate food plant and lay eggs thereon. Such a haphazard approach requires deposition of thousands of eggs.

Members of another vast group of species, including most of the Tachininae, broadcast their eggs in places likely to be visited by the host, usually a food plant that has already sustained damage. Larvae hatching from these eggs remain in ambush, waiting until they can attach themselves to, and burrow into, a suitable passing host. To minimize desiccation, these larvae, which may have to wait many days, are covered with small sclerites that fit together like a suit of armor. Not surprisingly this group of Tachininae has the widest range of hosts, many of them hidden by day. These hosts include Orthoptera, Dermaptera, Embioptera, and Lepidoptera, as well as Chilopoda and Arachnida.

Members of a third large group of Tachinidae, belonging to the tribe Dexiini *sensu lato*, and including the Australasian Rutiliini, also broadcast their eggs; but the hatchlings burrow into the substrate on which they were deposited, either soil, rotten wood, or the host's frass (if the host is a burrower or miner), and actively search for the host. A few genera of Goniinae do this as well. For example, newly hatched larvae of *Lixophaga* Townsend and *Lydella* Robineau-Desvoidy can successfully parasitize wood and stem borers by depositing their eggs at openings made by the host; the first instar is then left to burrow through the host's frass to make final contact.

At least eight orders of insects, as well as centipedes, serve as hosts. Larvae of Lepidoptera probably support the majority of species of Tachinidae; most members of the large subfamilies Tachininae and Goniinae attack lepidopterous larvae.

True bugs (Hemiptera–Heteroptera, particularly Pentatomidae, Coreidae, Nabidae, and Lygaeidae) are parasitized almost exclusively by the Phasiinae. The egg-laying apparatus of some exotic phasiines is the most complex in the family; but because all phasiines deposit or inject unembryonated eggs, the subfamily is assumed to be one of the more primitive groups of Tachinidae.

Both adults and larvae of Coleoptera serve as hosts to various genera of tachinids. Larvae of Scarabaeidae, Cerambycidae, and Elateridae, which are invariably buried in soil or rotten wood, are sought out by first instars of Dexiini. Adult scarabs are attacked by members of the tribe Palpostomatini, as well as those of the blondeliine genus *Cryptomeigenia* Brauer & Bergenstamm. Adult Carabidae may be parasitized by species of *Zaira* Robineau-Desvoidy and *Freraea* Robineau-Desvoidy. The first instars of *Cryptomeigenia* and *Zaira* have saw-like teeth on the anterior edge of the labrum, presumably for cutting through the tough cuticle of their hosts. *Zaira eleodivora* (Walton) has also been reared from a tenebrionid, a beetle group noted for its tough cuticle. Both adults and larvae of the Chrysomelidae are heavily attacked by various Blondeliini. Even a few weevils are parasitized. Weevil larvae hidden within roots, stems, fruits, or nuts are sought out by burrowing first instars of *Gnadochaeta* Macquart. Adult weevils are parasitized through the mouth while feeding by the female of *Rondania* Robineau-Desvoidy.

Orthopteroid orders also serve as hosts for a miscellaneous collection of genera. Best known are the Acemyiini, which deposit embryonated eggs directly on grasshoppers. The tachinine genera *Ormia* Robineau-Desvoidy and *Glaurocara* Thomson are crepuscular or nocturnal, ovolarvipositing on or near long-horned grasshoppers and crickets of the families Gryllidae, Gryllotalpidae, and Tettigoniidae (Crosskey 1965, Cade 1975). Females of *Ormia* are attracted to the songs of singing males; they may even be attracted to a loudspeaker reproducing a recording of the call notes of the appropriate host (Cade 1975). Species of the blondeliine genus *Anisia* Wulp deposit minute fully embryonated eggs, each enclosed in a gelatinous capsule, on potential food of crickets and cave crickets. Members of the genus *Phasmophaga* Townsend, which have been reared from walkingsticks, apparently oviposit in a similar fashion and this habit, when more fully investigated, may prove to be a synapotypy of *Anisia* and *Phasmophaga* and perhaps of *Meigenielloides* Townsend as well. Another unrelated tachinid, *Dichocera orientalis* (Coquillett), has been reared from cave crickets (Silberglied, personal communication). The walkingstick, *Diapheromera femorata* (Say), is also parasitized by *Euhalidaya genalis* (Coquillett); females of this species run about over the dorsum of the walkingstick, depositing fully embryonated eggs at random on its cuticle. Mantids are attacked by the mainly Neotropical genus *Masiphya* (Thompson 1963, Guimarães 1966); some large mantids have even survived the parasitic encounter (Heitzmann-Fontenelle and Guimarães 1966). Even cockroaches are not immune from attack. In the Neotropics they are attacked by females of *Calodexia* Wulp when marauding columns of army ants flush them from their hiding places; the females of *Calodexia* accompany the advancing ant columns, along with females of the phasiine genus *Androeuryops* Beneway and conopids of the genus *Stylogaster* Macquart, to take advantage of the ants' ability to uncover potential hosts (Rettenmeyer 1961). Some species of *Calodexia* may not be dependent on army ants to find their prey, however, for one species has been taken in the highlands of Mexico where such ants apparently do not occur.

Dermaptera in Europe are attacked by two tachinids, the tachinine *Triarthria spinipennis* (Meigen) and the goniine *Ocytata pallipes* (Fallén). *T. spinipennis* has been successfully introduced into Newfoundland and the Pacific Northwest to combat the introduced European earwig in those areas, and it has evidently spread to New England (Woodley, personal communication). Even the small order Embioptera has its share of tachinid parasites, most of which are undescribed (Arnaud 1963, personal communication).

Although larvae of Diptera have generally escaped parasitism by tachinids, those of Tipulidae and Tabanidae, both of which are soil dwellers, are regular hosts of a few genera. Tipulid larvae are attacked by species of *Admontia* Brauer & Bergenstamm and of *Siphona*, which apparently seek out the exposed spiracular plates of the hosts and deposit their embryonated eggs directly on them, and by members of *Allophorocera* Hendel, which deposit microtype eggs, presumably in situations where tipulid larvae are feeding. *Phasiops flavus* Coquillett and three species of *Billaea* Robineau-Desvoidy have been reared from larvae of *Tabanus* and *Hybomitra* (Hayes 1958; Teskey 1969; Burger, personal communication).

The only noninsects to be parasitized are centipedes, in addition to a single unpublished record each for a spider and a scorpion. In North America, *Lypha harrisi* (Reinhard) was reared from an unidentified species of geophilid centipede. A European species, *Loewia foeda* (Meigen), which parasitizes the common European centipede, *Lithobius forficatus* (Linnaeus), appeared recently in eastern United States (Wood and Wheeler 1972) and southern Ontario (Arnaud, personal communication).

Among the Hymenoptera, members of several genera of tachinids have been reared from leaf-feeding larvae of sawflies. The only other Hymenoptera parasitized by tachinids are adult ants, attacked by a rare European species, *Strongygaster globosa* (Meigen), and colonial wasps, whose nests are infested in the New World by members of the genus *Ophirion* Townsend and by a species of *Lixophaga*. The various species of *Ophirion* are presumed to deposit fully embryonated eggs at the entrances of the nests, leaving their newly hatched larvae to make their own way to the brood chambers. In the Afrotropical, Oriental, and Australian regions, social wasps are also parasitized, but by quite unrelated genera of tachinids belonging to the tribe Anacamptomyiini (Crosskey 1973, 1976, 1980). Adults of all these wasp-parasitizing species are pale in coloration (a characteristic associated with a variety of crepuscular and nocturnal tachinids). Possibly they escape their hosts' defences by ovipositing at or after dusk.

Hyperparasitism by one tachinid on another has apparently not been recorded. However, hyperparasitism by the tachinids *Nemorilla floralis* (Fallén) and *Bessa selecta* (Meigen) on an ichneumonid, *Cephaloglypta laricis* Momoi, has been reported from Japan (Kamijo 1973).

Adult Tachinidae are usually among the most active of insects, seldom remaining still long enough to be captured easily. This hyperactivity usually serves to distinguish them from adult sarcophagids, especially the Sarcophaginae, which they resemble to some extent; the latter are sedentary by comparison. Adult tachinids probably all require daily access to a source of sugar. Flowers, especially composites of the genera *Aster, Solidago, Chrysanthemum,* and *Erigeron,* as well as many others south of the Nearctic region, are avidly visited by the large Tachinini, as well as by Phasiinae, some Dexiini, and some Goniini. Nevertheless, honeydew seems to be the preferred food source for most Nearctic species, and a greater array may be collected at honeydew than at flowers. In the spring, before the leaves have appeared, sap flowing from tree wounds provides sugar for such early species as those of *Gonia* Meigen. If protein is required in the adult diet, it seems not to be needed in quantity, for adults have been kept in cages for several weeks on honey alone.

Males of many tachinids are conspicuous among the many different kinds of insects that aggregate on hilltops, a phenomenon called hilltopping (McAlpine and Munroe 1968). This behavior is now generally interpreted as a mechanism for the meeting of the sexes, for mated pairs are only encountered at aggregation sites. On almost any sunny morning or early afternoon throughout the spring and summer, various species may be encountered on hilltops, each species occupying a particular spot. So precise is this spot that a given species may be found year after year in exactly the same place, waiting on the same shrub, or even the same branch of that shrub. Selection of such precise sites, year after year, by successive generations of tachinids must be instinctive, and presumably must be visually determined by characteristics of the foliage and topography of the hilltop rather than by olfactory cues. Females are seldom seen at these sites, but may occasionally be found waiting there, probably when males are not present at that moment. As has been found for oestrids (which have been more intensively studied, see Ch. 107), females are probably intercepted by a waiting male the instant they arrive at the site; therefore not surprisingly they are seldom collected.

The behavior of hilltopping male tachinids is of two types, evidently depending on whether they use their eyes or their antennae predominently in recognizing a potential female. Both types can be found together in the same genus. Those species that seem to rely on vision have a narrower frons, i.e. larger eyes, than the female of that species, while their antennae usually do not differ appreciably from those of the female. These males can be seen resting on foliage or on tree trunks in an apparently alert stance, always head down if on a vertical surface. Each male chases any passing object, including other males of their species or other insects, even those much larger than themselves. Bright sunlight seems to be a prerequisite for this activity. If the object pursued proves not to be a female of the same species, the male usually returns to his original perch or to another leaf or portion of tree trunk nearby, and again takes up a waiting stance. Those species that apparently do not rely on vision have their eyes and frontal widths essentially the same as those of their respective females; their antennae, however, specifically the third flagellomeres, are demonstrably longer than those of the female. It is to this group that all species with subdivided third flagellomeres belong (Fig. 2.45). Males of these species do not aggregate at a waiting station and consequently are much more difficult to collect or study. Nevertheless, several species have been observed and collected as they visit specific sites, usually tips of prominent branches, tops of isolated shrubs and other landmarks, hilltops, or prominent isolated tree trunks. On cool mornings these males occasionally land on their specific site, perhaps to sun themselves briefly; but such visits are usually so brief that they are easily overlooked. Bright sunlight may not be as important to this group of species as it is for the visually oriented ones. As with the waiting males, these flying males may be collected at precisely the same sites year after year, and such sites must be selected visually by the flies by instinct according to topography.

Males assembled at an aggregation site are usually seen chasing one another. This activity has often been interpreted as territorial behavior, an incorrect assumption in my opinion, at least as far as the Tachinidae are concerned. Among other families, for example, species of *Cuterebra* Clark, a male patrolling an area most likely to be visited by females may gain some advantage by repelling competitors. However, if an aggregation site is indeed selected visually by instinct, many males of a given species will all assemble there, and if their predominent behavior is to chase any passing object in anticipation of intercepting a female, they are likely to end up chasing one another. Although this behavior does indeed appear to be aggressive interaction, I have not seen one individual tachinid succeed in repelling another; instead they instantly lose interest in each other and return to their waiting stations once physical contact is made. Studies with butterflies performing similarly have shown that males have very little power of discrimination between different passing objects (Tinbergen 1958). Such interactions between males, even if not territorial, are at least wasteful of energy and a group of males sharing the same aggregation site will usually ignore each other until one departs rapidly from its respective place, inciting all the others to follow in hot pursuit.

Not all male Tachinidae aggregate on hilltops. In mountainous terrain, a few species may, indeed, be found on the highest peaks, but smaller side peaks and ridges may be equally favored. In these areas some species also aggregate in the valleys, on foliage alongside rivers or streams, and on prominent sunlit tree trunks, in situations analogous to those on hilltops. Males of a few species, in particular those of *Gonia,* seem to search at random throughout their particular habitat; although evidence is lacking, these species may be able to detect females from a distance.

Host-seeking gravid females may be encountered almost any time of the day, whether the sun is shining or not, frantically scurrying over and under foliage. Selection of an appropriate habitat and host plant must precede actual host seeking, or much time would be wasted searching in unproductive areas. For those species laying microtype eggs, or those depositing waiting or searching larvae, selection of an appropriate habitat must be critical, for powers of dispersal of first instars must be quite limited, even for those that must burrow into the host's substrate. Insufficient research has been done into the habits of host-seeking female Tachinidae, and into the stimuli that guide them ultimately to their hosts. However, Monteith (1955, 1956, 1958*a*, 1958*b*, 1960) showed that host-plant odor was probably the primary factor in attracting *Bessa harveyi* (Townsend) to its host. Other factors, such as host odor and host movement, subsequently acted as stimulants. Odors of nonhost plants in the vicinity exerted a negative effect and in nature may help to protect some host colonies.

Classification and distribution. The family Tachinidae may be the second largest family of Diptera in number of described species in the Nearctic region, second only to the Tipulidae. Perhaps 8000 species have been described world wide, over 1200 of these from the Nearctic region. From other faunal regions many hundreds more await description in the major museums. An accurate count of described species is unattainable at present; many supposedly valid names may, after revision, turn out to be synonyms.

As a group adults are readily characterized among calyptrates by the presence of meral bristles and a well-developed subscutellum. Members of only two genera (*Litophasia* Girschner and *Tarassus*, neither found in the Nearctic region) lack meral bristles, and a small, mostly Neotropical group of genera, including *Bezzimyia*, have such a weak subscutellum that they could be confused with Rhinophoridae or Calliphoridae such as *Angioneura* Brauer & Bergenstamm. Nearly all adult tachinids have a distinct bend in M (Fig. 191), a character they share with sarcophagids, oestrids, and calliphorids. Most sarcophagids, but few tachinids, have three prominent longitudinal dark stripes on the scutum; tachinids tend to have four stripes (i.e. the midline is pale) or none (although *Nemorilla* Rondani and *Billaea* are notable exceptions). Most calliphorids have blue or green metallic bodies, but members of two tachinid genera, *Gymnocheta* Robineau-Desvoidy and *Chrysotachina* Brauer & Bergenstamm, are as brilliantly metallic green as any calliphorid.

Characters of the mouthparts of first-instar larvae provide a convincing synapomorphy attesting to the monophyly of the Tachinidae: the anterior end of the cephalopharyngeal skeleton, which is assumed to be the labrum that has become broadly fused to the rest of the cephalopharyngeal skeleton, extends anteriorly as a single hook-like or axe-like beak, while the mandibles are not recognizable and are presumably vestigial, present as lateral sclerites. In the Sarcophagidae, the labrum, if well-developed as in Miltogramminae and Paramacronychiinae, is articulated with the cephalopharyngeal skeleton and the mandibles are distinct and usually well-developed, with hooked apices.

Although the family appears to be a monophyletic unit, and, by and large, is readily defined and universally recognized, there is no consistent classificatory scheme within the family. By an unfortunate accident of fate, early specialists in the Tachinidae, from Robineau-Desvoidy (1863) to Townsend (1934–1942), have been more concerned with differences than with similarities. This perspective has resulted in finer and finer splitting at the generic level. Proliferation of genera by these authors became an end in itself, at the expense of a deeper understanding of higher levels of classification. Because of the superficial heterogeneity in appearance of many adult tachinids, few stable taxonomic characters have been found that may be depended upon to indicate relationships. Instead, Townsend used various permutations and combinations of the presence or absence of bristles but made little use of their relative size or arrangement. Unfortunately, there are only a limited number of possible combinations of presence or absence relative to the many thousands of extant species and most of them do not seem to serve as a basis for understanding relationships or building a stable classification. Descriptions of new taxa, even today, sometimes neglect to mention unique features, but instead, present further combinations or recombinations of the same limited suites of characters. Furthermore, these character suites are usually not correlated with internal structure, life cycle, larval characters, or other character states; instead, they appear, presumably by convergence or parallel development, in various genera that seem unrelated on other characters of terminalia or developmental stages. Such convergence, multiplied many times over because of the vast number of superficially similar species, has resulted in a long history of incorrect identifications and misunderstandings of relationships, a trend that still continues. A classification based on shared derived character states is badly needed but will be difficult to develop and may be long in coming. This need is now being met by research into internal structures, terminalia, larvae, and life cycles. However, much remains to be discovered, and even the most recent classifications still rely mainly on arrangements of bristles and probably contain few monophyletic taxa.

Four subfamilies, Phasiinae, Tachininae, Dexiinae, and Goniinae, are recognized here, corresponding in most respects to classifications proposed in several recent treatments, for example those of Herting (1960, 1984), Mesnil (1944–1975), and Crosskey (1973, 1976, 1977, 1980), but with some important differences. Namely, several tribes that Mesnil and Crosskey included in the Tachininae have been shifted here to the Dexiinae. The small subfamily Dufouriinae of these authors has also been combined here with the Dexiinae because of the shared presence of a special type of hinged aedeagus (discussed below), believed to be a synapomorphy of the subfamily. Classification of the Tachinidae into four subfamilies differs in some important respects from the arrangement proposed by Townsend (1934–1942) on which the subsequent Nearctic (Sabrosky and Arnaud 1965) and Neotropical (Guimarães 1971) catalogs were based, although the composition of the Phasiinae is essentially the same.

Members of the Phasiinae show the greatest diversity of adult structure of any group of Tachinidae. Some are bee or wasp mimics, although they fall far short of the Syrphidae in this respect. All Phasiinae, except *Strongygaster* Macquart, lay unincubated eggs on bugs (Hemiptera–Heteroptera), and this is virtually the sole justification for the taxon. The possession of a uterus by *Strongygaster*, coupled with ovolarviposition on beetles and ants rather than bugs, is itself evidence that this genus may not be a member of the Phasiinae. Unfortunately, there are apparently no morphological characters that are common to all members of this assemblage.

The Tachininae and Goniinae cannot be separated at present. Most species with a setose prosternum have been placed in the Goniinae, but there are ample exceptions, including some species in which this character is variable. The tribe Siphonini has been placed in the Tachininae by Herting (1960) and in the Goniinae by Mesnil and Crosskey; its members have a setose prosternum, as in Goniinae, but in other features the group resembles Tachininae more than Goniinae. Several other, otherwise typical Tachininae have a setose prosternum (e.g. *Hystricia*, *Macromya* Robineau-Desvoidy, and some *Lypha*), and there are some genera whose position is not evident.

All members of the Tachininae possess a uterus and deposit eggs ready to hatch. Although species of a few genera deposit eggs directly on the host (e.g. *Macquartia* and *Cleonice* on chrysomelid larvae), the majority seem to scatter their maggots about in a potential host's habitat, leaving host-finding to the larva or to chance encounter by a passing host. In the male terminalia of tachinines, the surstyli are usually widely separated and syntergosternite 7 + 8 is often large and bulbous.

A small minority of genera of Goniinae, including all members of the tribes Exoristini and Winthemiini, the genera *Aplomya* and *Prooppia* Townsend, and a few genera of Blondeliini (*Belida*, *Medina*, and *Meigenia*), deposit unincubated eggs on their hosts. The remaining members of the subfamily all have a uterus and all deposit fully embryonated eggs ready to hatch; their relationship to those above that lack a uterus is problematic. Among those with a uterus, all members of a large group deposit microtype eggs, minute, limpet-shaped eggs that are scattered over the host's food plant, especially where it has been recently damaged. An egg does not hatch until eaten by the host, stimulated to do so by enzymes in the host's foregut. The newly hatched larva penetrates the gut wall to take up its initial position within the body. This complex of characters and behavior is surely a synapotypy, by which this group of genera can be recognized as a monophyletic unit; but unfortunately it cannot be recognized on external characters, except for the globose female abdomen enlarged in most genera to accommodate the large number of eggs developing therein. The remaining Goniinae that do not produce microtype eggs are a diverse lot that probably do not form a single monophyletic group; their interrelationships need much additional study.

The Dexiinae is the only subfamily that can be defined on the basis of a synapomorphy. The aedeagus is hinged (Fig. 261) presumably between basiphallus and distiphallus, and the apex of the basiphallus extends beyond the hinge as a tapering prolongation. The gonopod lacks setae and is reduced to a strap-like supporting sclerite at the base of the aedeagus, and has, at most, a small conical point instead of the usual ventrally projecting portion. The parameres are usually closely applied to the basal part of the aedeagus, usually ending at about the same point as the apex of the basal part of the aedeagus. As here constituted, the Dexiinae includes all species with this type of male terminalia, thus corresponding closely only with the subfamily of the same name of Herting (1960, 1984); it encompasses tribes such as the Palpostomatini, Phyllomyini, Thelairini, Voriini, and Wagneriini, which are included in Tachininae by Mesnil and Crosskey. Two quite different species have been regarded as type species of *Dexia* Meigen, and application has been made to the International Commission on Zoological Nomenclature for fixation of a type species. The uncertain status of the genus, however, has no bearing on the name of the subfamily, for as used here and by Herting (1960, 1984), both taxa to which the name has been applied have the same type of aedeagus and therefore belong to the same subfamily.

Tachinidae are abundant on all continents and on all of the larger continental islands. The faunas of the largest islands, such as New Zealand, New Guinea, and Madagascar, are rich in endemic genera and species; the origins of only the tachinid fauna of New Zealand have been discussed (Dugdale 1969). However, their diversity dwindles rapidly as one proceeds along island chains away from the larger islands and continents. The larger islands of Polynesia have a moderate number of species, but on Hawaii tachinids are known only as introductions and are rare or absent on small remote oceanic islands. Greenland has only five species, all shared with, and presumably derived from, adjacent Ellesmere Island. Bermuda, Iceland, Spitzbergen, and the Soviet Arctic Islands (except Wrangell Island) apparently lack tachinids. The Pribilof Islands have only two recorded species, and the Aleutian Islands seem to be devoid of them. The West Indies (with the notable exception of Trinidad) are likewise impoverished when compared with the large and diverse faunas of the adjacent Neotropical region.

Key to genera[2]

1. Prosternum setose (Figs. 153, 154), sometimes sparsely so 2

Prosternum without setae (Fig. 155)[3] 175

2. Scutum with five or more postsutural supra-alar bristles, two anterior to largest bristle; first bristle arising close to transverse suture; second bristle smallest and displaced medially (Fig. 162) 3

Scutum with three or four postsutural supra-alar bristles, only one anterior to largest bristle; first bristle arising more or less equidistant between transverse suture and second bristle (Figs. 163–165) 9

3. Anepimeron with an exceptionally long bristle extending posteriorly beyond middle of lower calypter (Figs. 215, 216). Anterior and posterior lappets of posterior thoracic spiracle about equal in size, each with a fringe of plumose hairs enclosing a narrow V-shaped opening at or near middle of spiracle (Fig. 169) 4

Anepimeron with shorter bristles not extending to middle of lower calypter or with none. Anterior and posterior lappets of posterior thoracic spiracle unequal; the posterior one larger, forming a crescent-shaped opening with anterior lappet (Fig. 170) 7

4. Dorsal surface of lower calypter, except for a narrow band along posterior margin, covered with long erect hairs (Fig. 215) .... ***Hystricia*** Macquart, in part[4]

2 spp.; widespread

Dorsal surface of lower calypter without long erect hairs (Figs. 216, 217) 5

5. Abdominal tergite 3 with only one pair of median marginal bristles (as in Fig. 231). Body bright metallic green or blue .... ***Chrysotachina*** Brauer & Bergenstamm

2 spp.; widespread; Curran 1939

Abdominal tergite 3 with more than one pair of median marginal bristles (Fig. 233) 6

6. Abdominal tergites 3 and 4 each with numerous scattered discal bristles (Fig. 234); abdomen black. Parafacial setose on upper half or more .... ***Bombyliomyia*** Brauer & Bergenstamm

1 sp., *soror* (Williston); western

Abdominal tergites 3 and 4 each with a single transverse row of discal bristles (Fig. 233); abdomen metallic purplish or greenish. Parafacial bare at least on lower half .... ***Chlorohystricia*** Townsend

1 sp., *cyaneiventris* (Wulp); Arizona

7. Thorax, abdomen, and most of head metallic green or blue. First postsutural intra-alar bristle about as close to transverse suture as first dorsocentral bristle; outer basal bristle of postpronotum not accompanied by a smaller posteromedially placed bristle .... ***Gymnocheta*** Robineau-Desvoidy, in part

4 spp.; widespread; Brooks 1945*a*

Thorax, abdomen, and head without metallic green integument. First postsutural intra-alar bristle almost as close to transverse suture as first postsutural supra-alar bristle and much closer to suture than first postsutural dorsocentral bristle (Fig. 162); outer basal bristle of postpronotum with a smaller bristle posteromedial to it 8

8. Outer third of lower calypter with pale recumbent hairs dorsally. Medial surface of fore coxa entirely covered with short appressed setae, arranged in a longitudinal band of black setae bordered by pale setae (Fig. 153). Large species, over 10 mm in length, with broad orange abdomen .... ***Macromya*** Robineau-Desvoidy

1 sp., *crocata* Reinhard; Arizona, Texas; Reinhard 1968*b*

Lower calypter with a few pale recumbent hairs confined to outer margin only. Medial surface of fore coxa bare (as in Fig. 154). Size various, with abdomen brown, gray, or bluish, tesselated .... ***Xanthophyto*** Townsend, in part

2 spp.; widespread

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[2] Only native genera, and those successfully introduced, occurring north of Mexico, are included.

[3] Any specimen with a single hair, or pair of hairs, may be an atypical member of either group and should be keyed out under both couplet 2 and couplet 175.

[4] Including *H. testaceiventris* Wulp, and species formerly placed in *Bombyliopsis* Townsend.

9. First postsutural supra-alar bristle at least as long and stout as first postsutural dorsocentral bristle (Fig. 163) 10

First postsutural supra-alar bristle shorter and finer than first postsutural dorsocentral bristle (Figs. 164, 165) 96

10. Ocellar bristles reclinate or lateroclinate (Figs. 2–4) 11

Ocellar bristles proclinate or absent (as in Figs. 5–10) 17

11. Parafacial bare (as in Figs. 6–8) .... ***Distichona*** Wulp, in part[5]
3 spp.; widespread

Parafacial setose (as in Figs. 2–5) 12

12. Eye covered with conspicuous dense hairs, each hair longer than combined diameter of four or more eye facets (Figs. 2, 5–10). Lower part of parafacial with patch of fine hairs (Fig. 2) .... ***Distichona*** Wulp, in part
see couplet 11

Eye apparently bare (Figs. 3, 4). Parafacial with coarse hairs or bristles or both over most of its length 13

13. Facial ridge with dense row of short stout decumbent bristles along almost its entire length, flanked ventrally by two rows of shorter bristles (Fig. 3) ..... ***Chaetocrania*** Townsend
1 sp., *antennalis* (Coquillett); southwestern

Facial ridge with fewer bristles, with, at most, a single row of bristles on lower two-thirds or less (as in Fig. 2) 14

14. Katepisternum with four bristles arranged in a transverse row, the bristle next to the anteriormost in line with the other three (Fig. 178); apical scutellar bristles horizontal, thin and decurved .... ***Eucnephalia*** Townsend
1 sp., *gonoides* Townsend; southwestern

If katepisternum with four bristles, then the one next to the anteriormost is displaced ventrally out of line with the other three (as in Figs. 176, 177); apical scutellar bristles usually inclined upward 15

15. Parafacial with an even row of four or more bristles adjacent to ptilinal fissure, isolated from smaller remaining parafacial setae (Fig. 4). Second aristomere usually 10 or more times as long as wide, and usually more than half as long as third aristomere (Fig. 4). Male with proclinate orbital bristles (as in Fig. 20) .... ***Gonia*** Meigen
29 spp.; widespread; Morrison 1940, Brooks 1944*a*

Parafacial with scattered setae; if those nearest ptilinal fissure appear larger, then they are distant from fissure by at least half their length and do not form an even row. Second aristomere usually less than five times as long as wide and usually less than half as long as third aristomere 16

16. Three or more upper orbital bristles usually present, arranged in an arc with the innermost reclinate and the outermost lateroclinate (Fig. 20); male with proclinate orbital bristles. Head yellow in ground color, with yellow or silvery pollen, contrasting with dark sparsely pruinose body .... ***Onychogonia*** Brauer & Bergenstamm
4 spp.; northern and western, Arctic-alpine; Brooks 1944*a*

One or two reclinate upper orbital bristles present (Fig. 21); male without proclinate orbital bristles. Head and body gray or silvery pruinescent, not contrasting .... ***Spallanzania*** Robineau-Desvoidy[6]
6 spp.; widespread

17. Eye covered with conspicuous dense hairs (Figs. 5–12) 18

Eye apparently bare (hairs usually present, but so sparse and short as to be easily overlooked, each hair no longer than combined diameter of two facets) (as in Figs. 13–19) 57

18. Postpronotum with middle basal bristle displaced anterolaterally forming a nearly right-angled triangle with outer and inner basal bristles (Fig. 157); middle basal bristle also arising lateral to a line between outer basal and outer anterior bristles 19

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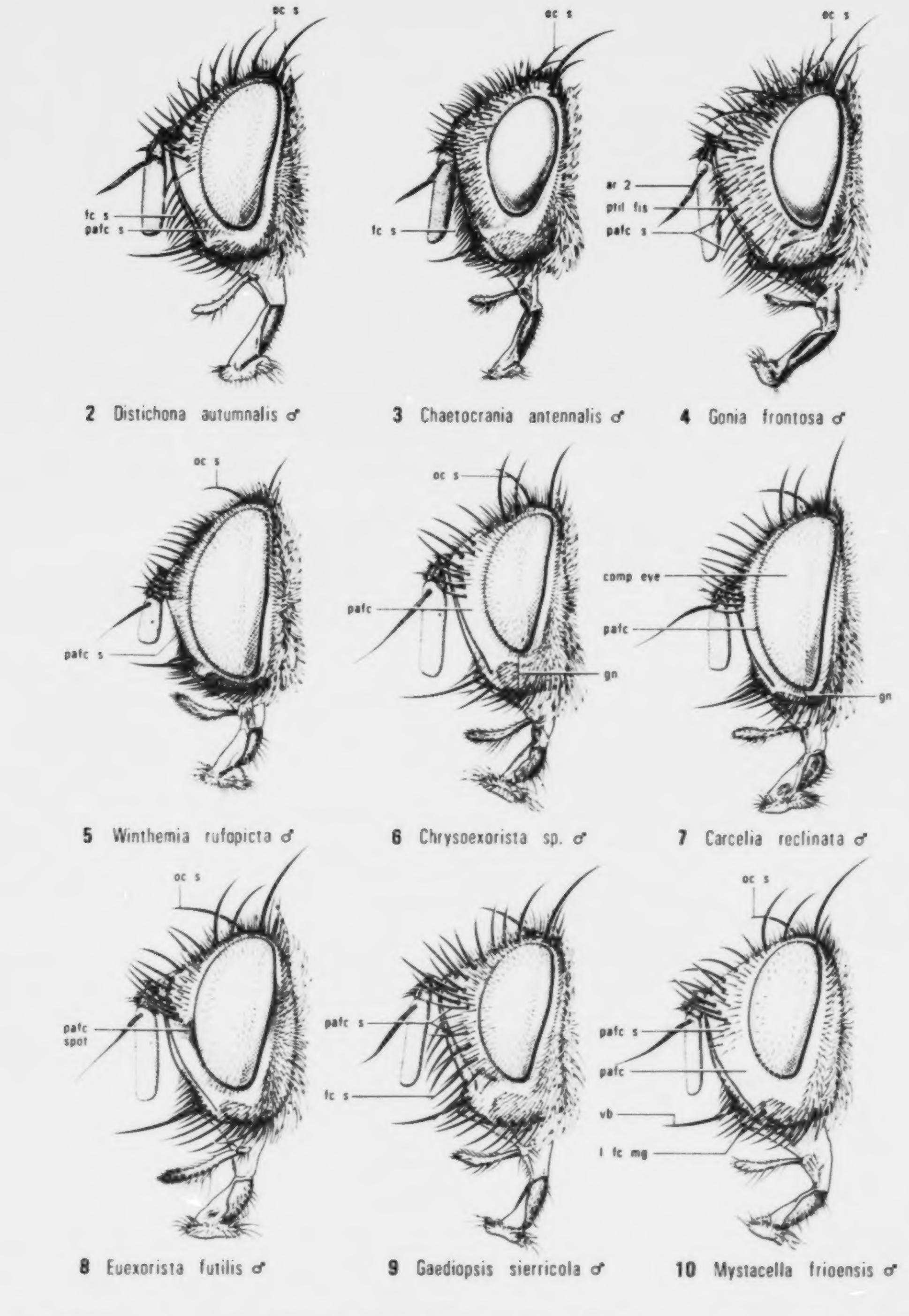
[5] Also included here are species formerly placed in *Aravaipa* Townsend and *Olenochaeta* Townsend.

[6] Also included here are species formerly placed in *Acroglossa* Williston and *Imaguncula* Reinhard.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oc s
pafc s
pafc
vb
l fc mg

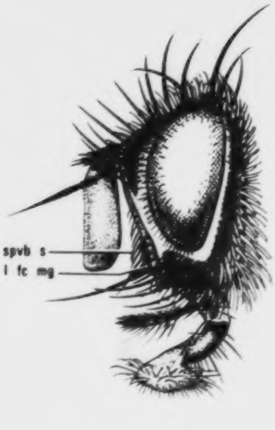
2 Distichona autumnalis ♂ 3 Chaetocrania antennalis ♂ 4 Gonia frontosa ♂

5 Winthemia rufopicta ♂ 6 Chrysoexorista sp. ♂ 7 Carcelia reclinata ♂

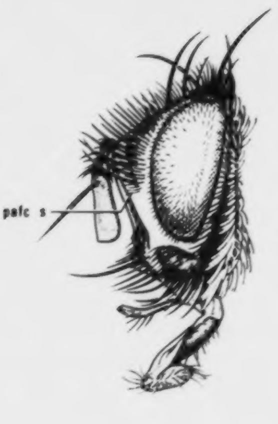
8 Euexorista futilis ♂ 9 Gaediopsis sierricola ♂ 10 Mystacella frioensis ♂

Figs. 110.2–10. Lateral views of head: (2) *Distichona autumnalis* (Townsend); (3) *Chaetocrania antennalis* (Coquillett); (4) *Gonia frontosa* Say; (5) *Winthemia rufopicta* (Bigot); (6) *Chrysoexorista* sp.; (7) *Carcelia reclinata* (Aldrich & Webber); (8) *Euexorista futilis* (Osten Sacken); (9) *Gaediopsis sierricola* (Townsend); (10) *Mystacella frioensis* (Reinhard) (*continued*).

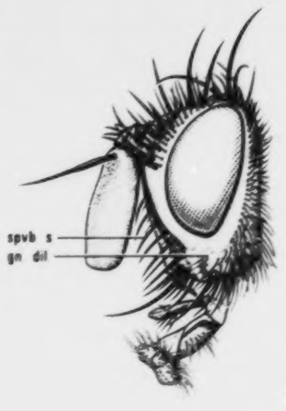
Abbreviations: ar, aristomere; comp eye, compound eye; fc s, facial seta; gn, gena; l fc mg, lower facial margin; oc s, ocellar bristle; pafc, parafacial; pafc s, parafacial seta; ptil fis, ptilinal fissure; vb, vibrissa.



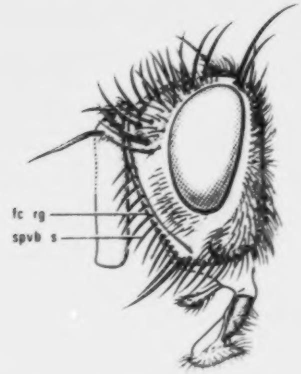
11 Phryxe pecosensis ♂



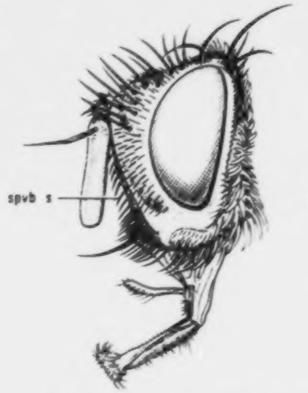
12 Eunemorilla longicornis ♂



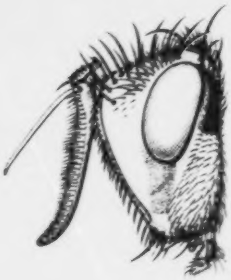
13 Erynnia condecens ♂



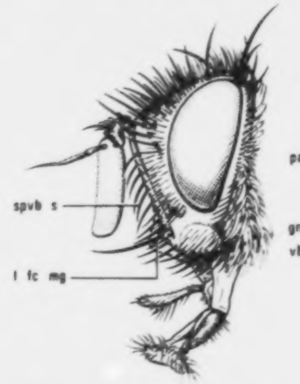
14 Eleodiphaga pollinosa ♂



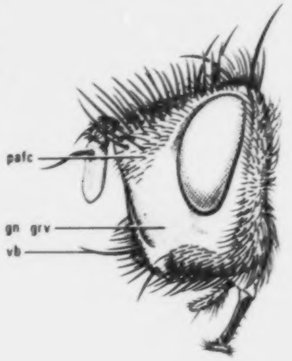
15 Torosomyia parallela ♂



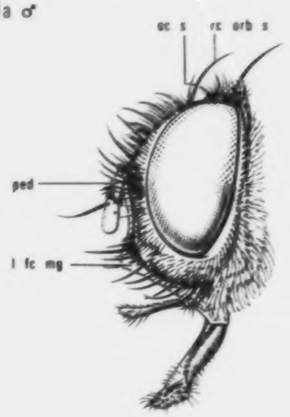
16 Oraphasmophaga pictipennis ♂



17 Chaetogaedia analis ♂



18 Asseclamyia sphenofrons ♂



19 Atactopsis reinhardi ♂

Figs. 110.11–19. Lateral views of head (*continued*): (11) *Phryxe pecosensis* (Townsend); (12) *Eunemorilla longicornis* (Reinhard); (13) *Erynnia condecens* Reinhard; (14) *Eleodiphaga pollinosa* Walton; (15) *Torosomyia parallela* Reinhard; (16) *Oraphasmophaga pictipennis* (Reinhard); (17) *Chaetogaedia analis* (Wulp); (18) *Asseclamyia sphenofrons* Reinhard; (19) *Atactopsis reinhardi* Sabrosky & Arnaud (*continued*).

Abbreviations: fc rg, facial ridge; gn dil, genal dilation; gn grv, genal groove; l fc mg, lower facial margin; oc s, ocellar bristle; pafc, parafacial; pafc s, parafacial seta; ped, pedicel; rc orb s, reclinate orbital bristle; spvb s, supravibrissal bristle; vb, vibrissa.

Postpronotum with middle basal bristle more or less in line with outer and inner basal bristles (Fig. 158), or with inner basal bristle absent (Fig. 156); if middle basal bristle forming an apparent angle with outer and inner basal bristles, this angle at least 160°; middle basal bristle usually medial to a line between outer basal and outer anterior bristles (latter not always present) 34

19. Katepimeron haired, at least on its anterior two-thirds (Fig. 169) 20

Katepimeron bare, or with at most three or four hairs on anterior fourth 25

20. Parafacial with hairs on upper half or more (Fig. 5) 21

Parafacial bare on lower two-thirds or more (Figs. 6–8) 22

21. Hairs on abdominal tergites 3 and 4 recumbent. Katepisternum rarely with more than two bristles .... ***Winthemia*** Robineau-Desvoidy, in part[7]

27 spp.; widespread; Guimarães 1972, Sabrosky 1973 (females)

Hairs on abdominal tergites 3 and 4 erect, at right angles to surface of tergite. Katepisternum with three bristles .... ***Diotrephes*** Reinhard

1 sp., *atriventris* (Walker); eastern U.S.A.

22. Facial ridge with bristles on at least lower third or more (as in Figs. 2, 9) .... ***Hemisturmia*** Townsend[8]

2 spp.; widespread

Facial ridge bare on all but lowest fifth 23

23. Parafacial with a few proclinate hairs below lowest frontal bristle ..... ***Chesippus*** Reinhard

1 sp., *notialis* Reinhard; Arizona

Parafacial entirely bare below lowest frontal bristle 24

24. Abdominal tergites 3 and 4 each with median discal bristles (as in Fig. 231). Scutum with a median dark longitudinal stripe and a paired lateral stripe .... ***Nemorilla*** Rondani

3 spp.; widespread; Aldrich and Webber 1924

Abdominal tergites 3 and 4 without median discal bristles. Scutum with pale median stripe and two pairs of longitudinal stripes .... ***Orasturmia*** Reinhard[9]

1 sp., *vallicola* Reinhard; Arizona, Texas

25. Facial ridge with row of long erect bristles on lowest two-thirds or more (as in Figs. 14, 35) .... ***Patelloa*** Townsend

10 spp.; widespread; Aldrich and Webber 1924 (as *Phorocera*, in part)

Facial ridge with at most a row of hair-like decumbent setae on lower half or less 26

26. Hind coxa with one or more setae on posteroapical margin (Fig. 228) .... ***Hyphantrophaga*** Townsend, in part[10]

10 spp.; widespread; Sellers 1943 (in part)

Hind coxa bare on posteroapical margin (hairs arising on first abdominal segment may, in profile, appear to arise on coxa) 27

27. Gena exceptionally narrow; distance between eye and lower cranial margin less than one-tenth total height of head (as in Fig. 7) .... ***Eumasicera*** Townsend, in part[11]

5 spp.; widespread

Gena broader; distance between eye and lower cranial margin more than one-ninth height of head (as in Fig. 8) 28

28. Pruinescence of frons and most of thorax and abdomen, in life, vivid metallic green or yellowish green, fading soon after death to a yellowish brown that may be temporarily restored to its metallic luster by application of alcohol or a petroleum solvent; abdomen with transverse black bands. Gena exceptionally high, with the distance between eye and lower cranial margin, when seen in profile, one-fifth or more total height of head (Fig. 6) .... ***Chrysoexorista*** Townsend

5 spp.; western; Sellers 1943 (as *Zenillia*, in part)

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[7] Included here is *Timavia fumiferanae* (Tothill), placed by Sabrosky and Arnaud (1965) in *Omotoma* Lioy. *Timavia* Robineau-Desvoidy is regarded here as only a subgenus of *Winthemia*.

[8] Included here is *Pseudolomyia scissilis* Reinhard.

[9] Included here is *Angustiopsis saginata* Reinhard.

[10] Also included here are species formerly placed in *Eusisyropa* Townsend.

[11] Also included here are species formerly placed in *Houghia* Coquillett and *Pacidianus* Reinhard, as well as *setinervis* (Coquillett), a species unplaced to subfamily by Sabrosky and Arnaud (1965).

Pruinescence of body mostly or entirely gray, without metallic green color, and gena narrower, less than one-fifth of height of head (except in *Hyphantrophaga scolex* (Reinhard); a Californian species with large globose uniformly ochrous brown abdomen and orange antenna) 29

29. Palpus black 30

Palpus brown, yellow, or orange 32

30. Facial ridge with slender decumbent setae on lower third to half, the length of this row more than half length of palpus (Fig. 140). Egg microtype (as in Fig. 266) .... **Myxexoristops** Townsend, in part[12]
2 spp.; widespread

Facial ridge with only a few small setae on lower fourth or less (as in Fig. 8); length of this row less than half length of palpus 31

31. Facial ridge thickened, slate gray, contrasting with adjacent brassy-pruinescent parafacial; parafacial slightly concave just below lowest frontal bristle; pruinescence at this point appearing as a shiny spot when illuminated from below, or as a dark spot when illuminated from above (Fig. 8). Male lacking an outer vertical bristle. Egg microtype (as in Fig. 266) .... **Euexorista** Townsend
1 sp., *futilis* (Osten Sacken); widespread

Facial ridge narrow, not contrasting with adjacent parafacial in color; parafacial without concave area just below lowest frontal. Male with outer vertical bristle. Egg unembryonated planoconvex (as in Fig. 264) .... **Prooppia** Townsend
1 sp., *crassiseta* (Aldrich & Webber); eastern

32. Facial ridge with slender decumbent setae on lower third to half; the length of this row more than half length of palpus (Fig. 140). Egg microtype (as in Fig. 266) .... **Myxexoristops** Townsend, in part
see couplet 30

Facial ridge with only a few small setae on lower fourth or less (as in Fig. 8); length of this row less than half length of palpus 33

33. Mid tibia with one anterodorsal bristle (as in Fig. 221), or if with two, then the larger bristle is proximal and the smaller one is distal. Abdominal tergites 3 and 4 each with at most one pair of discal bristles. Abdomen globose, especially in female, as deep as wide, enclosing terminalia within a slit-like opening (Fig. 246) (except in *angustata* (Wulp), of Arizona and Texas, which may not belong here). Facial ridge straight or slightly convex in profile, except just above vibrissa (as in Fig. 14). Cerci of male without interlocking teeth at apices. Egg microtype (as in Fig. 266) .... **Hyphantrophaga** Townsend, in part[13]
see couplet 26

Mid tibia with two or more anterodorsal bristles, with the largest the most distal (as in Fig. 222). Abdominal tergites 3 and 4 usually with more than one pair of discal bristles; abdominal tergite 5 enclosing a rounded or triangular opening, not concealing terminalia. Facial ridge concave in profile. Cerci of male with medially directed interlocking teeth at apices (Fig. 263). Egg planoconvex, embryonated *in utero* ...... **Phebellia** Robineau-Desvoidy, in part[14]
8 spp.; widespread; Sellers 1943 (as *Aplomya*, in part)

34. Parafacial with setae on upper half or more (Figs. 9, 10) 35

Parafacial bare, or with at most a few hairs below lowest frontal bristle 37

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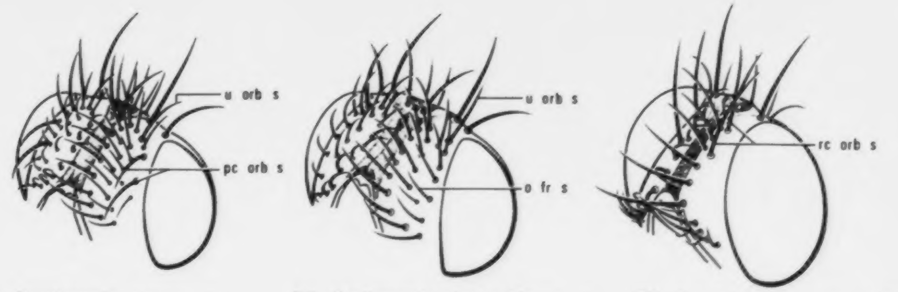
[12] Included here are two species, *fronto* (Coquillett) and *neurotomae* (Sellers), formerly placed in *Aplomya* by Sellers (1943) and Sabrosky and Arnaud (1965).

[13] This is a provisional placement for three rather distinct Nearctic species, *angustata* (Wulp), *blandita* (Coquillett), and *scolex* (Reinhard), that were previously placed in *Zenillia* Robineau-Desvoidy by Sellers (1943) and Sabrosky and Arnaud (1965). They differ from other members of *Hyphantrophaga* in lacking setae on the hind coxa. Their ultimate generic placement requires comparative studies of additional related Neotropical Goniini.

[14] This is a provisional placement for the following: *curriei* (Coquillett) and *erecta* (Sellers), formerly placed in *Thelymyia* Brauer & Bergenstamm by Sellers (1943) and Sabrosky and Arnaud (1965), as well as *cerurae* (Sellers), *epicydes* (Walker), *helvina* (Coquillett), *imitator* (Sellers), *pheosiae* (Sellers), and *trichiosomae* (Sellers), formerly placed by these authors in *Aplomya*.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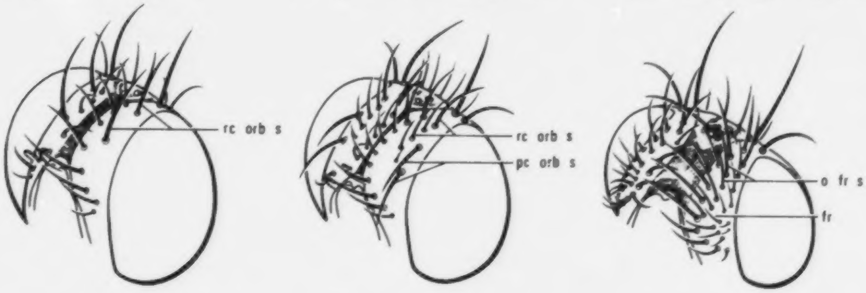
20 Onychogonia magna ♂ **21** Spallanzania hesperidarum ♂ **22** Pseudochaeta venusta ♂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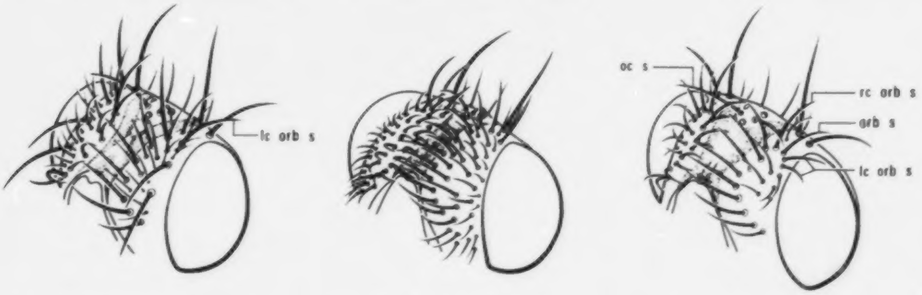
23 Pseudochaeta argentifrons ♂ **24** Pseudochaeta pyralidis ♂ **25** Clemelis triseta ♂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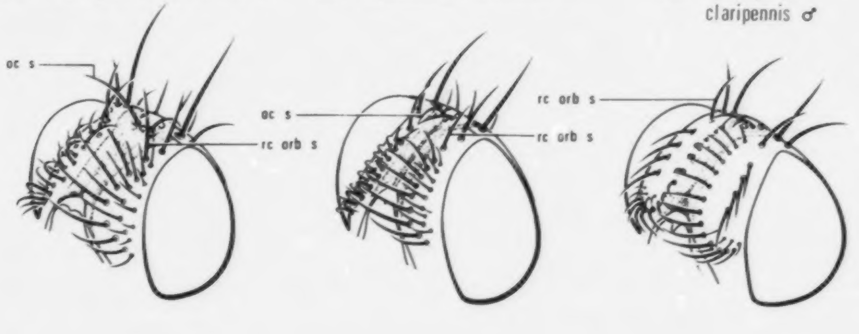
26 Chaetoglossa picticornis ♂ **27** Myatelemus trossulus ♂ **28** Gymnophryxe claripennis ♂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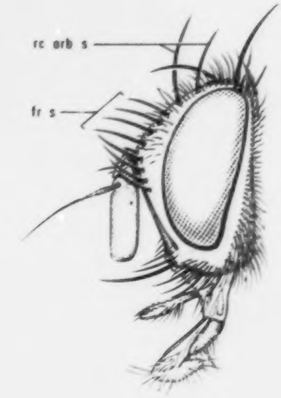
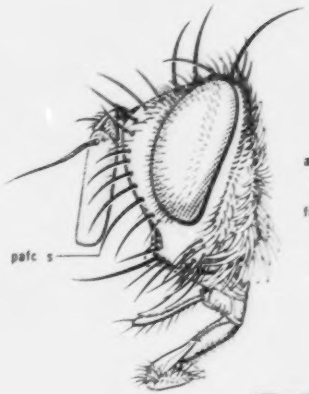
29 Lydella thompsoni ♂ **30** Drino rhoeo ♂ **31** Atacta brasiliensis ♀

Figs. 110.20–31. Oblique anterior views of frons: (20) *Onychogonia magna* Brooks; (21) *Spallanzania hesperidarum* (Williston); (22) *Pseudochaeta venusta* (Reinhard); (23) *Pseudochaeta argentifrons* Coquillett; (24) *Pseudochaeta pyralidis* Coquillett; (25) *Clemelis triseta* (Villeneuve); (26) *Chaetoglossa picticornis* Townsend; (27) *Myatelemus trossulus* (Reinhard); (28) *Gymnophryxe claripennis* (Reinhard); (29) *Lydella thompsoni* Herting; (30) *Drino rhoeo* (Walker); (31) *Atacta brasiliensis* Schiner (*continued*).

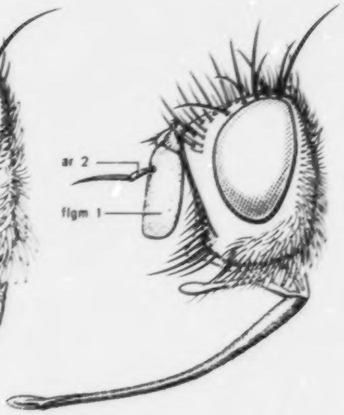
Abbreviations: fr, frons; lc orb s, lateroclinate orbital bristle; o fr s, outer frontal bristle; oc s, ocellar bristle; orb s, orbital bristle; pc orb s, proclinate orbital bristle; rc orb s, reclinate orbital bristle; u orb s, upper orbital bristle.



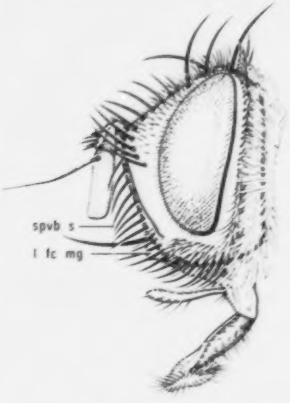
32 Ametadoria harrisinae ♂



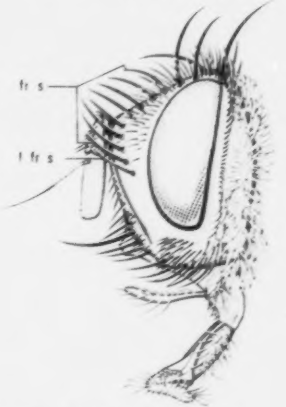
33 Paradidyma affinis ♂



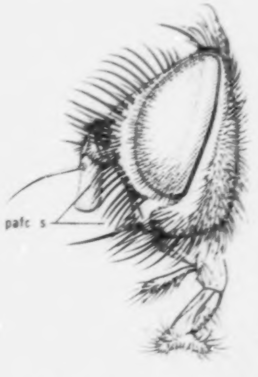
34 Eucoronimyia hastata ♀



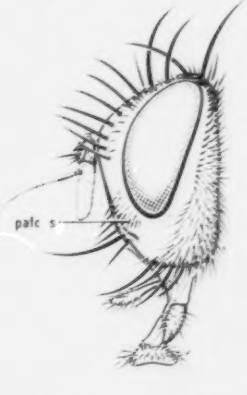
35 Chetogena tachinomoides ♂



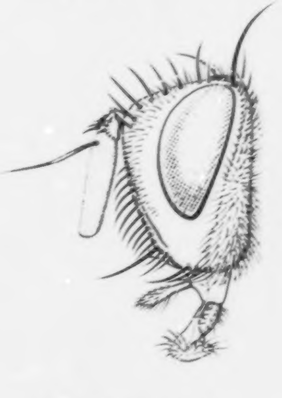
36 Exorista larvarum ♂



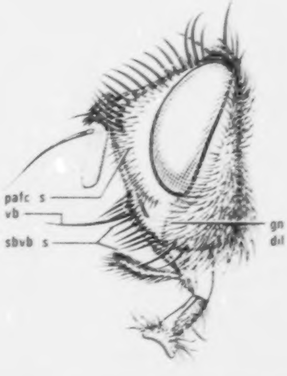
37 Eulasiona comstocki ♂



38 Vibrissina hylotomae ♂



39 Istocheta aldrichi ♂



40 Cryptomeigenia theutis ♂

Figs. 110.32–40. Lateral views of head (*continued*): (32) *Ametadoria harrisinae* (Coquillett); (33) *Paradidyma affinis* Reinhard; (34) *Eucoronimyia hastata* (Coquillett); (35) *Chetogena tachinomoides* (Townsend); (36) *Exorista larvarum* (Linnaeus); (37) *Eulasiona comstocki* Townsend; (38) *Vibrissina hylotomae* (Coquillett); (39) *Istocheta aldrichi* (Mesnil); (40) *Cryptomeigenia theutis* (Walker) (*continued*).

Abbreviations: ar, aristomere; flgm, flagellomere; fr s, frontal bristle; l fr s, lower frontal bristle; gn dil, genal dilation; l fc mg, lower facial margin; orb, orbital; pafc s, parafacial bristle; rc orb s, reclinate orbital bristle; sbvb s, subvibrissal bristle; spvb s, supravibrissal bristle; vb, vibrissa.

35. Parafacial with vertical rows of erect setae of different sizes; these larger and bristle-like anteromedially, fine and hair-like posterolaterally (Fig. 9) .... ***Gaediopsis*** Brauer & Bergenstamm[15]
9 spp.; widespread

Parafacial setae of uniform size, all hair-like and decumbent (as in Figs. 5, 10) 36

36. Parafacial very broad, setose on upper half (Fig. 10); vibrissa arising above level of lower facial margin; ocellar bristles well-developed. Katepimeron bare .... ***Mystacella*** Wulp[16]
3 spp.; widespread; Reinhard 1930*b*

Parafacial narrow, setose along its entire length (Fig. 5); vibrissa level with lower facial margin; ocellar setae hair-like. Katepimeron entirely setose (as in Fig. 170) .... ***Winthemia*** Robineau-Desvoidy, in part[17]
see couplet 21

37. Hind coxa with one or more setae on posteroapical margin (Fig. 228) .... ***Carcelia*** Robineau-Desvoidy
12 spp.; widespread; Sellers 1943

Hind coxa bare on posteroapical margin 38

38. Apical scutellar bristles hair-like, parallel or divergent, or absent (Figs. 179, 180) .... ***Cyzenis*** Robineau-Desvoidy[18]
8 spp.; widespread

Apical scutellar bristles crossed (as in Figs. 182, 185) 39

39. Facial ridge setose on at least lower third (as in Figs. 11, 13–17) 40

Facial ridge bare except for a few recumbent setae on lowest third or less (as in Fig. 12) 48

40. Distance between eye and subcranial margin less than one-tenth height of head (as in Fig. 7). Frons with two or more large reclinate orbital bristles arising distinctly lateral to frontal row, the anteriormost arising near midlength of frons (Figs. 22–24); ocellar setae minute or absent .... ***Pseudochaeta*** Coquillett, in part[19]
11 spp.; widespread; Reinhard 1946*a*

Distance between eye and subcranial margin more than one-sixth height of head. Reclinate upper orbital bristles confined to posterior third of frons, usually arising behind uppermost frontal; ocellar bristles well-developed 41

41. Katepisternum with four or more bristles (Figs. 176, 177) 42

Katepisternum with three bristles (as in Fig. 174) 44

42. Facial ridge with fine recumbent setae (as in Fig. 15). M ending in R_{4+5} close to wing margin (as in Figs. 191, 201) .... ***Tsugaea*** Hall
1 sp., *nox* Hall; western

Facial ridge with stout erect supravibrissal bristles (as in Figs. 14, 15, 17). M ending separately in wing margin (as in Figs. 193–196) 43

43. Katepisternum with posteroventral bristle arising nearly in line with anterior and posterior bristles and nearly equidistant between the two; only the anteroventral bristle displaced ventrally (Fig. 176). Apical scutellar bristles directed posteriorly, almost horizontally .... ***Nilea*** Robineau-Desvoidy, in part[20]
8 spp.; widespread

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[15] Also included are species formerly assigned to *Gaediophana* Brauer & Bergenstamm.

[16] Also included are species formerly assigned to *Organomyia* Townsend and *Bolomyia* Brauer & Bergenstamm. *M. rufata* (Bigot) apparently does not occur north of Mexico and is not a synonym of *violacea* Wulp.

[17] This is a provisional placement for *antennalis* Coquillett, excluded from *Winthemia* by Guimarães (1972) and Sabrosky (1973). Although arrangement of postpronotal bristles is different from other species of *Winthemia*, the male terminalia and unembryonated planoconvex egg suggest a relationship, which may ultimately be resolved by additional study of the tribe Winthemiini.

[18] Also included are *Zenillia browni* Curran, as well as *anassa* Reinhard, *festinans* (Aldrich & Webber), *incrassata* (Smith), *mitis* (Curran), *regilla* (Reinhard), and *ustulata* (Reinhard), species that were not placed to genus by Sabrosky and Arnaud (1965).

[19] Also included are the species formerly placed in *Metopiops* Townsend and *Phaenopsis* Townsend.

[20] The species provisionally placed here include those formerly placed in *Clemelis* Robineau-Desvoidy and *Pseudoperichaeta* Brauer & Bergenstamm, as well as *halisidotae* (Aldrich & Webber), *dimmocki* (Webber), *lobeliae* (Coquillett), *valens* (Aldrich & Webber), and *victoria* (Aldrich & Webber), among species unplaced to genus by Sabrosky and Arnaud (1965).

Katepisternum with both posteroventral and anteroventral bristles displaced ventrally; the posteroventral bristle much closer to the posterior than to the anterior bristle (Fig. 177). Apical scutellar bristles erect, nearly at right angles to scutellum .... ***Lespesia*** Robineau-Desvoidy, in part
28 spp.; widespread; Beneway 1963, Sabrosky 1980

44. Katepisternal bristles arising quite close together; distance between anterior and posterior bristles less than three times distance between anterior and anteroventral bristles (Fig. 174) . . 45

Katepisternal bristles more dispersed; distance between anterior and posterior bristles more than three times distance between anterior and anteroventral bristles (Fig. 175) 46

45. Facial ridge with row of stout erect bristles (as in Fig. 14). Third aristomere thickened on basal three-quarters or more (as in Fig. 14) .... ***Madremyia*** Townsend
2 spp.; widespread

Facial ridge with finer more decumbent setae (Fig. 11). Third aristomere thickened on basal two-thirds or less .... ***Phryxe*** Robineau-Desvoidy
2 spp.; widespread

46. Bend of M nearly a right angle without a stub, or continuation of M (as in Fig. 191). Apical scutellar bristles directed posteriorly, almost horizontally. Frons with a single row of frontal bristles .... ***Nilea*** Robineau-Desvoidy, in part
see couplet 43

Bend of M either with a short stub (as in Fig. 192) or distinctly obtuse (as in Figs. 195, 196). Apical scutellar bristles inclined at 45° or more to horizontal, usually curving forward. Frons with extra row of bristles outside frontal row (Fig. 25) 47

47. Bristles of facial ridge slender, decumbent (as in Fig. 13). Frons, even of male, very broad (Fig. 25). Bend of M with short stub (as in Fig. 192). Arista thickened on basal three-quarters or more. Abdomen of female rounded apically, with short ovipositor .... ***Clemelis*** Robineau-Desvoidy
1 sp., *triseta* (Villeneuve); Yukon, Northwest Territories

Bristles of facial ridge stout, erect, and evenly spaced (as in Fig. 14). Frons, especially in male, narrower. Bend of M obtuse, without a stub (as in Fig. 195). Arista thickened only on basal half. Abdominal segment 5 of female pointed, with slender telescopic sharp-tipped ovipositor (Fig. 255) that is almost entirely concealed except for the sharp-tipped apex; apical segment, when extended, slender, straight, and as long as fore tibia ..... ***Acantholespesia*** n. gen.
3 spp., *comstocki* (Williston) (type species of genus), *signata* (Aldrich & Webber), and *texana* (Aldrich & Webber), all reared from stem-boring larvae of Cossidae, Megathymidae, Pyralidae, and Noctuidae (Arnaud 1978); southern

48. Katepisternum with four bristles arranged in a trapezoidal pattern (as in Fig. 177) 49

Katepisternum with two or three bristles (a fourth may rarely occur either between anterior and posterior bristles or ventral to anteroventral one, not forming a trapezoid) 50

49. Parafacial with a few hair-like setae below lowest frontal bristle (Fig. 12). Frons with one or more rows of bristles (o fr s) lateral to frontal row (as in Figs. 21, 25). All abdominal tergites with transverse bands of silvery pruinescence .... ***Eunemorilla*** Townsend[21]
5 spp.; western; Reinhard 1944*b* (as *Masiphyomyia*)

Parafacial bare below lowest frontal bristle (as in Figs. 11, 13). Frons with only scattered hairs outside frontal bristles. Abdominal tergite 5 of female and tergites 4 and 5 of male shining black except for narrow basal band of silvery pruinescence on tergite 4 .... ***Aplomya*** Robineau-Desvoidy
1 sp., *theclarum* (Scudder); widespread; Sellers 1943, in part

50. Vibrissa arising as far above lower facial margin as width of face between vibrissae (Fig. 149); ocellar setae absent. Katepimeron fully haired (as in Fig. 170); katepisternum with two bristles. Female ovipositor with piercer .... ***Mystacomyia*** Giglio-Tos
1 sp., *scordala* (Reinhard); Texas

Vibrissa arising at level of lower facial margin; ocellar bristles well-developed. Katepimeron bare on all but anterior end; katepisternum with three bristles. Female ovipositor tubular, without piercer 51

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[21] Included are species formerly placed in ***Masiphyomyia*** Reinhard and ***Mimologus*** Reinhard.

51. M ending in R_{4+5} well before reaching wing margin (Fig. 191)......... ***Tryphera*** Meigen
1 undescribed species; Yukon

M ending in wing margin (as in Figs. 193–196) 52

52. Palpus black or dark brown. Egg microtype (as in Figs. 266–268) 53

Palpus pale brown or yellowish. Egg planoconvex (unknown in *Aplomyopsis* Townsend) 54

53. Parafacial with several hairs below lowest frontal bristle (as in Figs. 10, 12) .... ***Eumea*** Robineau-Desvoidy
1 sp., *caesar* (Aldrich); widespread; Sellers 1943 (as *Aplomya*, in part)

Parafacial without hairs below lowest frontal (as in Figs. 11, 13) .... ***Platymya*** Robineau-Desvoidy[22]
2 spp.; widespread; Sellers 1943 (as *Aplomya*, in part)

54. Hind tibia with comb-like row of anterodorsal setae of rather uniform length, except for one longer bristle at midlength (Fig. 226). Abdominal tergites 2 and 3 each lacking median discal bristles .... ***Sisyropa*** Brauer & Bergenstamm
2 spp.; widespread; Sellers 1943

Anterodorsal setae of hind tibia uneven in length, alternating long and short. Abdominal tergites 2 and 3 each with scattered median discal bristles 55

55. Hind coxa with one or more setae on posteroapical margin (as in Fig. 228) .... ***Hubneria*** Robineau-Desvoidy
1 sp., *estigmenensis* (Sellers); widespread

Hind coxa bare on posteroapical margin 56

56. Apex of abdomen of male with a pair of circular patches of appressed hair arising from shiny black cuticle ventrally (female unknown) .... ***Aplomyopsis*** Townsend
1 sp., *polita* (Coquillett); southern

Apex of abdomen lacking such patches of appressed hair .... ***Phebellia*** Robineau-Desvoidy, in part
see couplet 33

57. Gena reduced to a narrow strip about one-twelfth height of head (as in Fig. 7) 58

Gena higher, at least one-tenth height of head (as in Figs. 8–10) 61

58. Hind coxa with one or more setae on its posteroapical margin (as in Fig. 228) .... ***Gymnocarcelia*** Townsend[23]
2 spp.; widespread

Hind coxa bare on posteroapical margin 59

59. Frons with two or more stout reclinate orbital bristles arising distinctly outside frontal row (Figs. 22–24); facial ridge with stout bristles on lower half or more; ocellar setae minute or absent .... ***Pseudochaeta*** Coquillett, in part
see couplet 40

Frons with reclinate orbital bristles more or less continuous with frontal row (as in Figs. 29, 30); facial ridge with fine hairs, or with a few bristles on lowest fourth, or bare; ocellar setae well-developed 60

60. Palpus inflated apically, with the swollen part bare (Fig. 138). Gena almost obliterated by lower margin of eye, scarcely visible in profile .... ***Hypertrophomma*** Townsend
1 sp., *opacum* Townsend; eastern

Palpus setose, not inflated apically (Fig. 139). Gena, although narrow, with both genal dilation and genal groove evident (as in Fig. 7) .... ***Eumasicera*** Townsend, in part
see couplet 27

61. M ending in R_{4+5} some distance from wing margin (Fig. 192) 62

M ending in wing margin separately from R_{4+5} (as in Figs. 193–196) 67

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[22] Included here are two species, *confusionis* (Sellers) and *trisetosa* (Coquillett), formerly placed in *Aplomya* by Sellers (1943) and Sabrosky and Arnaud (1965).

[23] Included here is *Elassomyia defecta* Reinhard, described from a specimen of *languida* (Walker) (senior synonym of *ricinorum* Townsend).

62. Proboscis elongate and very slender, longer than height of head (as in Figs. 34, 147). Posteriormost orbital bristle lateroclinate (Fig. 26). Postpronotum with only two bristles (Fig. 156) .... ***Chaetoglossa*** Townsend

1 sp., *picticornis* Townsend; central and southern

Proboscis not elongate, shorter than height of head. Posteriormost orbital bristle reclinate (as in Figs. 29–31). Postpronotum with three or more bristles (except in *Erynnia*) 63

63. Facial ridge bare on most of its length. M with stub or appendage extending beyond bend (Fig. 192) .... ***Hesperomyia*** Brauer & Bergenstamm

2 spp.; southwestern

Facial ridge bristled on most of its length. M without a stub or appendage (as in Figs. 191, 193) 64

64. Parafacial setose, exceptionally broad; facial ridge thickened, prominent in profile (Fig. 14) .... ***Eleodiphaga*** Walton

3 spp.; western

Parafacial bare. Facial ridge less prominent 65

65. Arista thickened only to midpoint (Fig. 13). Anterior margin of postgena convex, with distinct genal dilation .... ***Erynnia*** Robineau-Desvoidy

4 spp.; widespread; Reinhard 1968*a*

Arista thickened nearly to apex (Fig. 16). Anterior margin of postgena concave, evenly curved, without distinct genal dilation 66

66. Antenna orange, exceptionally long, slender, and anteriorly curved, long pilose in male (Fig. 16). Wing patterned .... ***Oraphasmophaga*** Reinhard

1 sp., *pictipennis* (Reinhard); Texas

Antenna dark, not as long or as slender as above, not curved forward. Wing transparent, milky, or evenly darkened .... ***Paraphasmophaga*** Townsend

2 spp.; southwestern

67. Anterodorsal bristles on hind tibia forming an even closely spaced row; each bristle separated from adjacent bristles by no more than three times its width (in female one bristle near middle of row usually slightly longer than the rest) (Figs. 225, 227) 68

Anterodorsal bristles on hind tibia irregular in length and spacing; each separated from adjacent setae by over three times its width (both sexes always with at least one much longer bristle near middle of row) 70

68. Abdomen black or dull dark brown without tesselated pattern of pruinescence. Anterodorsal setae of hind tibia nearly touching each other in both sexes (Fig. 225). Tergite 4 of male without patch of short dense hairs .... ***Leschenaultia*** Robineau-Desvoidy[24]

10 spp.; widespread; Brooks 1947 (as several genera)

Abdomen gray or brown, with tesselated pattern of pruinescence. Anterodorsal bristles on hind tibia usually more widely spaced (Fig. 227) 69

69. Katepisternum with four bristles (Fig. 177). Subvibrissal ridge with row of usually fewer than four bristles; this row less than half as long as length of row of setae on facial ridge. Abdomen of male without patches of short dense hair .... ***Lespesia*** Robineau-Desvoidy, in part

see couplet 43

Katepisternum with three bristles, the posteroventral one absent (as in Fig. 173). Subvibrissal ridge with evenly spaced row of more than four bristles; this row as long as row of setae on facial ridge. Tergite 4 of male with patch of short dense hairs (Fig. 247).......... .... ***Blepharipa*** Rondani[25]

2 spp.; eastern

70. Parafacial with setae over upper half or more (Figs. 15, 17–19) 71

Parafacial bare, or at most with a few hairs below lowest frontal bristle 77

71. Facial ridge with row of stout erect curved bristles on more than lower half (Fig. 17) ..72

Facial ridge with bristles confined to region of vibrissa (as in Fig. 18) 74

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[24] Also included are species formerly assigned to *Parachaeta* Coquillett.

[25] Also included is *Thysanomyia fimbriata* (Wulp), found in eastern U.S.A.

72. M ending in R_{4+5} before reaching wing margin (as in Fig. 191) .... ***Cloacina*** Reinhard
1 sp., *filialis* Reinhard; southwestern

M ending separately in wing margin 73

73. Bristles of facial ridge short (their length much less than width of parafacial) and closely spaced (Fig. 15); parafacial with small scattered hairs of uniform size ... ***Torosomyia*** Reinhard
1 sp., *parallela* Reinhard; Kansas

Bristles of facial ridge as long as width of parafacial, and more widely spaced (Fig. 17); parafacial with setae of different sizes .... ***Chaetogaedia*** Brauer & Bergenstamm
7 spp.; widespread

74. Parafacial relatively small, triangular, about as long as high (Fig. 18); genal groove correspondingly very large; vibrissa small, arising well above lower facial margin .... ***Asseclamyia*** Reinhard
1 sp., *sphenofrons* Reinhard; California

Parafacial narrower, setose nearly to lower margin; genal groove less conspicuous; vibrissa arising at level of lower facial margin 75

75. Fronto-orbital plate very broad, with three rows of medioclinate frontal bristles (Fig. 27). Second aristomere several times longer than wide .... ***Myatelemus*** Reinhard
1 sp., *trossulus* (Reinhard); Texas, Arizona

Fronto-orbital plate narrower, with one or at most two rows of medioclinate or reclinate frontal bristles. Second aristomere usually at most twice as long as wide 76

76. Ocellar setae small, less than half as long as reclinate orbital bristle (Fig. 19). Pedicel as long as first flagellomere. Notopleuron with a small extra bristle anterolateral to usual posterior bristle (Fig. 163) .... ***Atactopsis*** Townsend
1 sp., *reinhardi* Sabrosky & Arnaud; Texas

Ocellar setae nearly as long as either reclinate orbital bristle. Pedicel less than half as long as first flagellomere. Notopleuron with the usual two bristles .... ***Buquetia*** Robineau-Desvoidy
1 sp., *obscura* (Coquillett); widespread in U.S.A.

77. Facial ridge with erect bristles on lower half or more (as in Figs. 14–17) 78

Facial ridge bare, or with small recumbent setae on lower third 84

78. Ocellar setae absent 79

Ocellar setae well-developed, bristle-like (as in Figs. 28–30) 80

79. Katepisternum with three bristles forming a triangle (as in Figs. 173–175). All abdominal tergites gray pruinescent .... ***Heliodorus*** Reinhard
2 spp.; western

Katepisternum with four or more bristles (rarely three), arranged in a straight line (as in Fig. 178). Abdominal tergite 5 and often 4 also with gold or orange pruinescence .... ***Belvosia*** Robineau-Desvoidy[26]
14 spp.; widespread; Aldrich 1928

80. Anterior margin of postgena without a genal dilation (as in Fig. 16). Arista pubescent (Fig. 125) .... ***Prospherysa*** Wulp[27]
2 spp.; southern

Anterior margin of postgena with well-developed genal dilation (as in Figs. 11–13, 17–19). Arista apparently bare 81

81. Katepisternum with four bristles 82

Katepisternum with three bristles 83

82. Three or more upper orbital bristles present, arranged in an arc, with the innermost reclinate, the outermost lateroclinate, and those between inclined posterolaterally (Fig. 28) .... ***Gymnophryxe*** Villeneuve
1 sp., *claripennis* (Reinhard); western, Arctic-alpine

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[26] Also included are species formerly assigned to *Triachora* Townsend.

[27] These species were formerly assigned to *Epidexia* Townsend.

Upper orbital bristles reclinate; if more than one present, then bristles arranged in a longitudinal row .... ***Lespesia*** Robineau-Desvoidy, in part
see couplet 43

83. Abdomen almost entirely gold or grayish yellow pruinescent. Egg microtype (as in Fig. 266) .... ***Eufrontina*** Brooks
2 spp.; widespread

Abdomen black, with transverse gray pruinescent bands. Egg planoconvex .... ***Frontiniella*** Townsend
1 sp., *parancilla* Townsend; widespread

84. Postpronotum with middle basal bristle displaced anteriorly, forming a triangle with outer and inner basal bristles (as in Figs. 157, 159) 85

Postpronotum with middle basal bristle more or less in line with outer and inner basal bristles (as in Fig. 158), or inner basal bristle absent (as in Figs. 156, 161) 86

85. Lower facial margin sloping evenly forward from lower part of face, thus visible in lateral view below and in front of vibrissal angle (Fig. 141). Postpronotum with five large bristles arranged in a V (as in Fig. 157) .... ***Masiphya*** Brauer & Bergenstamm[28]
5 spp.; southern

Lower facial margin, if visible in profile, bent forward abruptly at level of vibrissal angle (as in Figs. 11, 17). Postpronotum with three large bristles, sometimes with one or two additional smaller ones anteriorly (as in Fig. 159) .... ***Allophorocera*** Hendel[29]
12 spp.; widespread; Curran 1927*c* (as *Erycia*)

86. Bifurcation of R_{2+3} and R_{4+5} with a single rather long seta on dorsal surface (Fig. 193) 87

Bifurcation of R_{2+3} and R_{4+5} with two or more small setae on dorsal surface 89

87. Katepisternum with three bristles. Fronto-orbital plate with a single row of frontal bristles; anterior reclinate orbital bristle larger than posterior one, with the two well-separated from each other (Fig. 32) .... ***Ametadoria*** Townsend
1 sp., *harrisinae* (Coquillett); widespread

Katepisternum with four bristles. Fronto-orbital plate with extra medioclinate bristles outside frontal row, usually forming a second row (Figs. 29, 30); two or three reclinate orbital bristles usually present, but if only two, then anterior one usually smaller than the posterior one (Fig. 30) 88

88. Ocellar bristles long, divergent (Fig. 28) .... ***Lydella*** Robineau-Desvoidy
3 spp.; widespread; Herting 1959

Ocellar bristles short, curving toward each other apically (Fig. 30), or absent .... ***Drino*** Robineau-Desvoidy
8 spp.; widespread

89. Postpronotum with only two bristles (as in Fig. 156); katepisternum with ventral bristle arising almost directly below anterior bristle. Uppermost orbital bristle lateroclinate. Bend of M broadly obtuse (Fig. 194) .... ***Masistylum*** Brauer & Bergenstamm
1 sp., *stenommatum* Wood; western, alpine

Postpronotum with three or more bristles; katepisternum with four bristles, or if with three, not arranged as above. Uppermost orbital bristle reclinate. Bend of M more acute ... 90

90. Notopleuron with one or more smaller bristles in addition to the usual two large ones (as in Fig. 163) .... ***Atacta*** Schiner
2 spp.; southeastern; Aldrich 1925*b*

Notopleuron with two bristles (as in Figs. 162, 164, 165) 91

91. Lower facial margin protruding in front of vibrissal angle when viewed laterally (as in Figs. 19, 141) .... ***Siphosturmia*** Coquillett[30]
8 spp.; widespread; Reinhard 1931, 1934*a*

Lower facial margin not visible in lateral view 92

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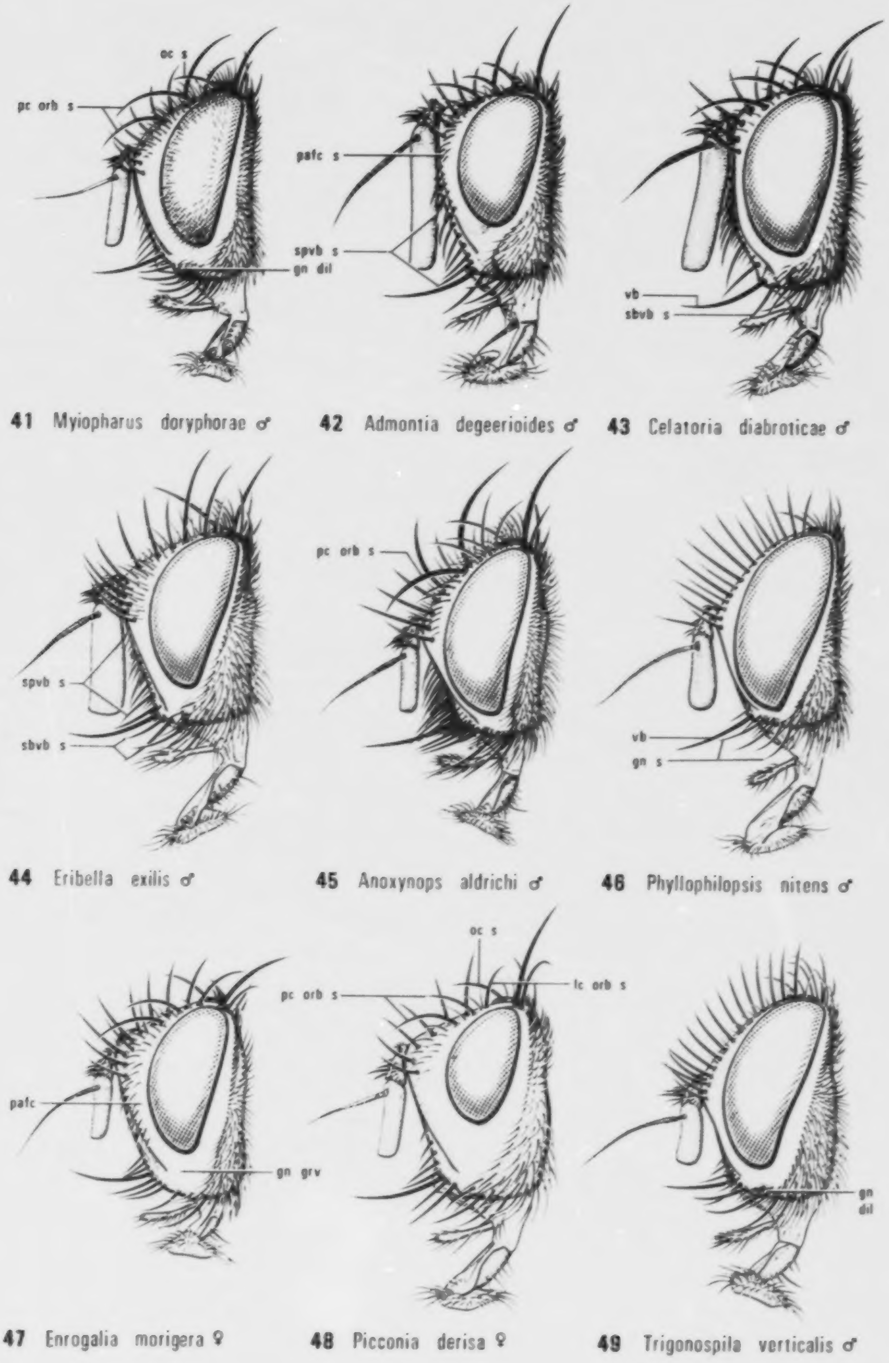
[28] Included here are all species placed by Sabrosky and Arnaud (1965) in the tribe Masiphyini.

[29] Included here are all species formerly placed in *Pilatea* Townsend.

[30] Also included is *Microsillus baccharis* (Reinhard).



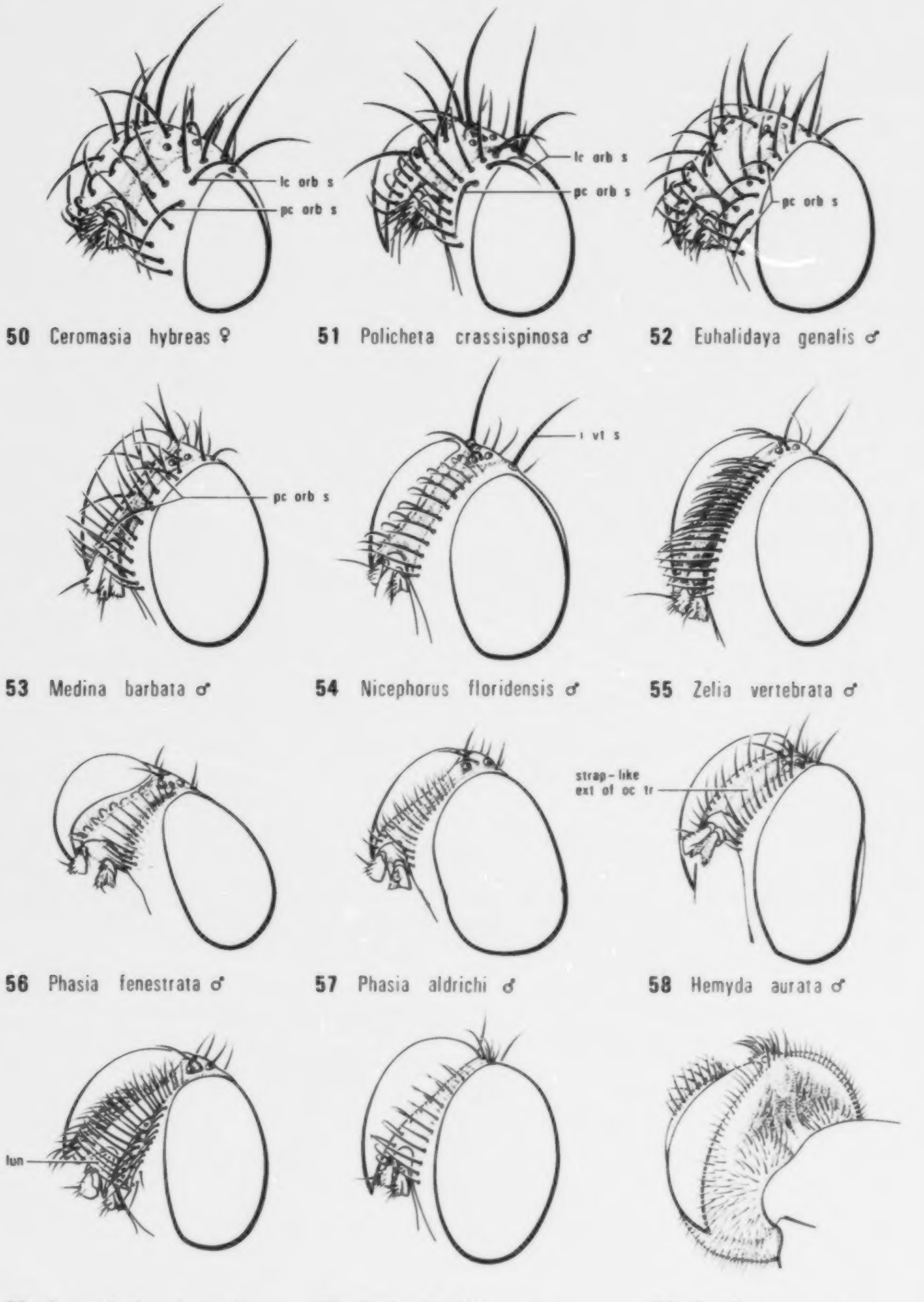
41 Myiopharus doryphorae ♂ **42** Admontia degeerioides ♂ **43** Celatoria diabroticae ♂

44 Eribella exilis ♂ **45** Anoxynops aldrichi ♂ **46** Phyllophilopsis nitens ♂

47 Enrogalia morigera ♀ **48** Picconia derisa ♀ **49** Trigonospila verticalis ♂

Figs. 110.41–49. Lateral views of head (*continued*): (41) *Myiopharus doryphorae* (Riley); (42) *Admontia degeerioides* (Coquillett); (43) *Celatoria diabroticae* (Shimer); (44) *Eribella exilis* (Coquillett); (45) *Anoxynops aldrichi* (Curran); (46) *Phyllophilopsis nitens* (Coquillett); (47) *Enrogalia morigera* Reinhard; (48) *Picconia derisa* (Reinhard); (49) *Trigonospila verticalis* (Reinhard) (*continued*).

Abbreviations: gn dil, genal dilation; gn grv, genal groove; gn s, genal seta; lc orb s, lateroclinate orbital bristle; oc s, ocellar bristle; pafc, parafacial; pafc s, parafacial bristle; pc orb s, proclinate orbital bristle; sbvb s, subvibrissal bristle; spvb s, supravibrissal bristle; vb, vibrissa.



50 Ceromasia hybreas ♀ **51** Policheta crassispinosa ♂ **52** Euhalidaya genalis ♂

53 Medina barbata ♂ **54** Nicephorus floridensis ♂ **55** Zelia vertebrata ♂

56 Phasia fenestrata ♂ **57** Phasia aldrichi ♂ **58** Hemyda aurata ♂

59 Oestrophasia clausa ♂ **60** Ormia dominicana ♂ **61** Opesia atrata ♂

Figs. 110.50–61. Oblique views of head: anterior views of frons (*concluded*) of (50) *Ceromasia hybreas* (Walker), (51) *Policheta crassispinosa* Wood, (52) *Euhalidaya genalis* (Coquillett), (53) *Medina barbata* (Coquillett), (54) *Nicephorus floridensis* Reinhard, (55) *Zelia vertebrata* (Say), (56) *Phasia fenestrata* (Bigot), (57) *Phasia aldrichi* (Townsend), (58) *Hemyda aurata* Robineau-Desvoidy, (59) *Oestrophasia clausa* Brauer & Bergenstamm, and (60) *Ormia dominicana* Townsend; (61) posterior view of back of head of *Opesia atrata* (Coquillett).

Abbreviations: i vt s, inner vertical bristle; lc orb s, lateroclinate orbital bristle; lun, lunule; pc orb s, proclinate orbital bristle.

92. Katepisternum with three bristles. Fronto-orbital plate with a few irregularly arranged bristles lateral to frontal row, some more than two-thirds length of longest frontal bristles (Fig. 50); female with only one proclinate orbital bristle; those behind it lateroclinate or reclinate (Fig. 50) .... ***Ceromasia*** Rondani

3 spp.; widespread

Katepisternum with four bristles. Fronto-orbital plate without bristles but with fine hairs lateral to frontal row (some small bristles less than half length of longest frontal bristle in *Zizyphomyia limata* (Coquillett)); female with two proclinate orbital bristles 93

93. Wing with anterior third darkly pigmented (Fig. 208). Mid tibia with a single anterodorsal bristle (Fig. 221) .... ***Myothyriopsis*** Townsend

1 sp., *picta* (Wulp); Texas

Wing without pigmented area. Mid tibia with more than one anterodorsal bristle (as in Figs. 222, 223) 94

94. Palpus flattened dorsoventrally; setae on its dorsomedial surface short, stout, rather appressed (Fig. 137) .... ***Euceromasia*** Townsend

5 spp.; widespread

Palpus cylindrical; setae on dorsomedial surface longer and more erect 95

95. Male with only one anterodorsal bristle on mid tibia and with patch of dense appressed hairs on ventral surface of abdominal tergite 4 (as in Fig. 247). Female with pointed, uniformly gray pruinescent abdomen .... ***Townsendiellomyia*** Baranov

1 introduced sp., *nidicola* (Townsend); northeastern U.S.A.

Male with two or more anterodorsal bristles on mid tibia, and either without patch of appressed hairs on abdomen or with extensive patches covering all of abdominal tergites 4 and 5 except for a middorsal longitudinal bare stripe. Female abdomen more rounded apically, with a basal pruinescent band on each tergite contrasting with dark apex .... ***Zizyphomyia*** Townsend[31]

3 spp.; widespread

96. Scutellum with three pairs of bristles; the lateral bristles longest, straight and divergent, arising about midway between the basal and apical bristles; apical bristles crossed (Fig. 183) 97

Scutellum usually with four pairs of bristles, with the lateral bristles arising more proximally between the basal and subapical bristles (Figs. 182, 185); if three pairs present (Fig. 184), then the lateral bristles are shorter than the apical bristles 100

97. Parafacial with vertical row of long stout erect bristles (Fig. 33) .... ***Paradidyma*** Brauer & Bergenstamm, in part[32]

16 spp.; widespread; Reinhard 1934*b*

Parafacial bare 98

98. Eye covered with conspicuous dense hairs; each hair longer than combined diameter of four or more eye facets; facial ridge with long erect bristles on lower half or more (as in Fig. 35) .... ***Neomintho*** Brauer & Bergenstamm[33]

2 spp.; eastern

Eye bare; facial ridge with fine decumbent setae on lower half or less 99

99. First flagellomere with conically pointed apex; second aristomere minute (Fig. 126). Proboscis not elongate. Facial ridge bare; genal bristles curving forward, in lateral view crossing subvibrissal bristles .... ***Ceracia*** Rondani

1 sp., *dentata* (Coquillett); widespread

First flagellomere rounded apically; second aristomere more than half as long as third aristomere. Proboscis long and slender (Fig. 34). Facial ridge with fine hairs on lower half or more .... ***Eucoronimyia*** Townsend

1 sp., *hastata* (Coquillett); southwestern

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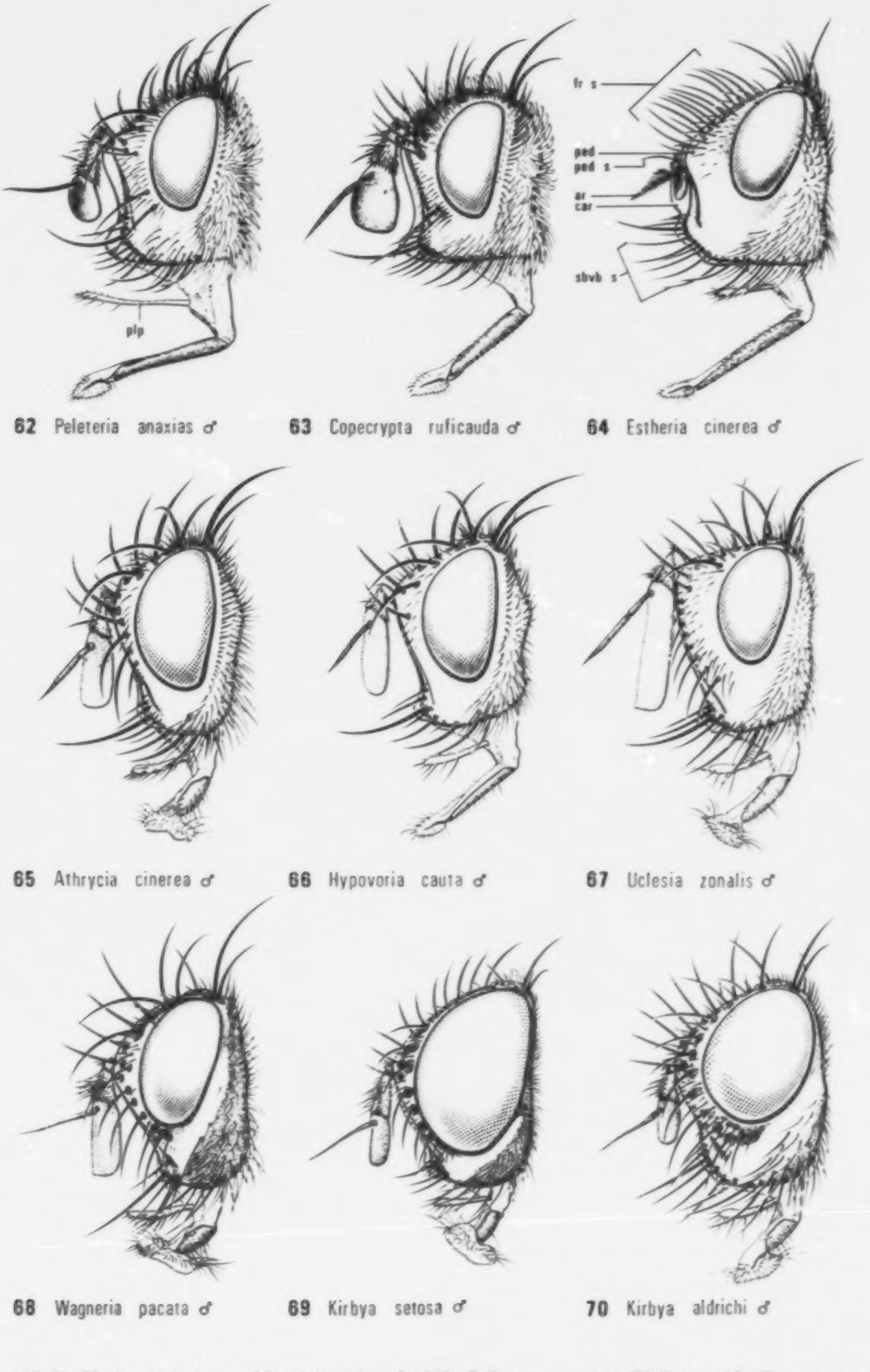
[31] Also included are *chihuahuaensis* (Townsend) (senior synonym of *chrysoprocta* (Reinhard), formerly placed in *Sturmia* Robineau-Desvoidy by Sabrosky and Arnaud (1965)) and *crescentis* (Reinhard), placed by these authors in *Drino*.

[32] Also included are all species placed by Sabrosky and Arnaud (1965) in *Atrophopalpus* Townsend, *Ceratomyiella* Townsend, and *Micromintho* Townsend.

[33] Included are both species placed by Sabrosky and Arnaud (1965) in the tribe Neominthoini.



62 Peleteria anaxias ♂ **63** Copecrypta ruficauda ♂ **64** Estheria cinerea ♂

65 Athrycia cinerea ♂ **66** Hypovoria cauta ♂ **67** Uclesia zonalis ♂

68 Wagneria pacata ♂ **69** Kirbya setosa ♂ **70** Kirbya aldrichi ♂

Figs. 110.62–70. Lateral views of head (*continued*): (62) *Peleteria anaxias* (Walker); (63) *Copecrypta ruficauda* (Wulp); (64) *Estheria cinerea* (Townsend); (65) *Athrycia cinerea* (Coquillett); (66) *Hypovoria cauta* (Townsend); (67) *Uclesia zonalis* Curran; (68) *Wagneria pacata* Reinhard; (69) *Kirbya setosa* (Townsend); (70) *Kirbya aldrichi* (Curran) (*continued*).

Abbreviations: ar, arista; car, carina; fr s, frontal seta; ped, pedicel; ped s, pedicellar seta; plp, palpus; sbvb s, subvibrissal bristle.

100. Ventral proepimeral bristle directed anteroventrally (Fig. 167). Base of R_{4+5} with a single large bristle (rarely with a smaller additional bristle); M ending at apex of wing (Fig. 196). Katepimeron usually with a single seta .... ***Phytomyptera*** Rondani[34]
23 spp.; widespread

If ventral proepimeral bristle directed anteroventrally and M ending at apex of wing (some *Chaetostigmoptera*), then base of R_{4+5} with several short bristles (Fig. 195) and katepimeron bare 101

101. At most only one frontal bristle arising below upper margin of pedicel (as in Fig. 64); pedicel with one or two long slender curved setae more than half as long as length of plumose arista; male with all frontal bristles proclinate (Fig. 97). M terminating in R_{4+5} well before wing margin, with a long extension beyond bend (as in Fig. 202) .... ***Microchaetina*** Wulp, in part[35]
8 spp.; western and southern; Reinhard 1942*a* (in part)

Frontal bristles usually descending below upper margin of pedicel (as in Fig. 63), but if not, then either pedicel without such long bristles or arista bare; male usually with some reclinate frontal bristles. M with at most a short extension, usually terminating in or near wing margin (Fig. 205) 102

102. Anepimeron with an exceptionally long bristle extending posteriorly beyond middle of lower calypter (Fig. 216). Anterior and posterior lappets of posterior thoracic spiracle about equal in size; each a fringe of plumose hairs, enclosing a narrow V-shaped opening at or near middle of spiracle (as in Fig. 169) 103

Anepimeron with shorter bristles not extending to middle of lower calypter or with none at all. Anterior and posterior lappets of posterior thoracic spiracle unequal; the posterior one larger, forming a crescent-shaped opening with anterior lappet (as in Fig. 170) 105

103. Dorsal surface of lower calypter, except for a narrow band along posterior margin, covered with long erect hairs (Fig. 215) .... ***Hystricia*** Macquart, in part
see couplet 4

Dorsal surface of lower calypter without long erect hairs 104

104. Abdomen with tesselated pattern of pruinescence ..... ***Lypha*** Robineau-Desvoidy, in part[36]
16 spp.; widespread

Abdomen shining black, usually with metallic greenish luster, each tergite without basal transverse pruinescent bands .... ***Lydina*** Robineau-Desvoidy
3 spp.; widespread

105. Lower calypter with a few pale recumbent hairs dorsally along outer margin .... ***Xanthophyto*** Townsend, in part
see couplet 8

Lower calypter bare dorsally, fringed only along margin 106

106. Bend of M a right angle; the portion beyond bend sinuous, curving toward apex (Fig. 197). An extra smaller bristle usually present between second and third postsutural supra-alar bristles (Fig. 164) 107

Bend of M obtuse; the portion beyond bend straight or convex (Figs. 195, 199, 200). No extra small bristle between second and third postsutural supra-alar bristles 116

107. Eye covered with conspicuous dense hairs (as in Fig. 6) 108

Eye apparently bare (as in Fig. 36) 112

108. Facial ridge with row of erect, widely and evenly spaced, stout bristles, usually on lower two-thirds or more (Fig. 35) 109

Facial ridge with small decumbent irregularly and more closely spaced setae, usually on lower half or less (Fig. 36) 110

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[34] Included here are the species formerly placed in *Acronarista* Townsend, *Apheloglutus* Greene, *Elfia* Robineau-Desvoidy, *Lispideosoma* Townsend, *Phasiostoma* Townsend, *Schizactia* Townsend, and *Schizotachina* Walker.

[35] Also included are all species formerly placed in *Reinhardiana* Arnaud and *Steveniopsis* Townsend.

[36] This is a provisional placement for all species formerly included in *Chromatocera* Townsend, *Exoristoides* Coquillett, *Helioplagia* Townsend, *Homalactia* Townsend, and *Plagiosippus* Reinhard. Their ultimate generic placement requires study of the tribe Polidiini (=Lyphini) on a world basis.

109. Lower margin of face not protruding, not visible in profile. Wing membrane flat at bend of M, not appearing as a continuation of M .... ***Austrophorocera*** Townsend[37]

9 spp.; widespread; Aldrich and Webber 1924 (as *Phorocera* subgenus *Parasetigena*, in part)

Lower margin of face protruding below vibrissal angle, visible in profile (Fig. 35). Wing membrane creased for a short distance distal to bend of M, appearing from above as a stub or continuation of M (Fig. 197) .... ***Chetogena*** Rondani[38]

16 spp.; widespread; Aldrich and Webber 1924 (as *Phorocera* subgenus *Parasetigena*, in part)

110. Lower margin of face not visible in profile .... ***Phorocera*** Robineau-Desvoidy, in part

8 spp.; widespread; Wood 1972

Lower margin of face protruding beyond vibrissal angle, visible in profile (as in Figs. 35, 36) 111

111. Facial ridge bristled on lower two-thirds or more (as in Fig. 36) .... ***Parasetigena*** Brauer & Bergenstamm

1 introduced sp., *silvestris* (Robineau-Desvoidy); northeastern U.S.A.

Facial ridge with bristles confined to lower third or less .... ***Chaetexorista*** Brauer & Bergenstamm

1 introduced sp., *javana* Brauer & Bergenstamm; Massachusetts

112. Facial ridge with row of stout erect bristles (as in Fig. 35) 113

Facial ridge with shorter decumbent bristles (Fig. 36) 114

113. Scutellum lacking apical bristles (as in Figs. 180, 184) .... ***Bessa*** Robineau-Desvoidy

2 spp.; widespread

Scutellum with crossed apical bristles (as in Fig. 185) .... ***Gueriniopsis*** Reinhard

1 sp., *setipes* (Coquillett); central and eastern

114. Frontal bristles descending to level of middle of facial ridge (Fig. 36) .... ***Exorista*** Meigen

5 spp.; widespread

Frontal bristles ending before reaching level of middle of facial ridge 115

115. Cerci of male spatulate in posterior view, broadest beyond middle. Sternite 7 of female with reflexed triangular piercer (Fig. 248) .... ***Phorocera*** Robineau-Desvoidy, in part

see couplet 110

Cerci of male slender, curved anteriorly, in posterior view broadest at base. Sternite 7 of female unmodified .... ***Tachinomyia*** Townsend

10 spp.; widespread; Curran 1926, Webber 1941

116. Apical scutellar bristles among the longest bristles on scutellum, at least as long as lateral scutellar bristles, arising close to midline, and crossing each other near their midlength (Fig. 181) 117

Apical scutellar bristles much shorter than sublateral or lateral scutellar bristles (Figs. 184–186) 118

117. Antennal bases separated, not touching each other (as in Figs. 83, 84, 86). End of M nearly perpendicular to R_{4+5} (Fig. 198) .... ***Graphogaster*** Rondani[39]

14 spp.; widespread; Brooks 1942 (as *Psalidopteryx*)

Antennal bases contiguous. End of M forming an acute angle with R_{4+5} or ending separately in margin .... ***Clastoneuriopsis*** Reinhard, in part

1 sp., *meralis* Reinhard; Washington; Brooks 1942

118. Subapical scutellar bristles divergent (Figs. 184–186) .... 119[40]

Subapical scutellar bristles convergent (Fig. 182) 167

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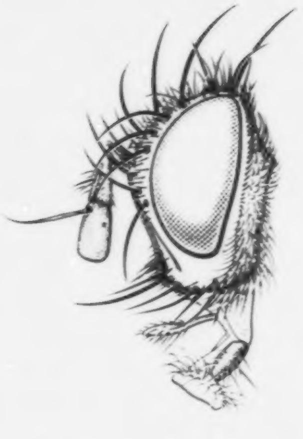
[37] This genus includes those species formerly included in *Euphoroceropsis* Townsend and *Palpexorista* Townsend (the former having priority over the latter).

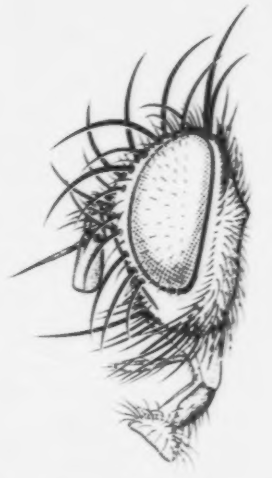
[38] Included here are all species formerly placed in *Euphorocera* Townsend, *Spoggosia* Rondani, and *Stomatomyia* Brauer & Bergenstamm.

[39] Included here are all species formerly placed by Sabrosky and Arnaud (1965) in the tribe Graphogastrini, except for the type species of *Clastoneuriopsis*.

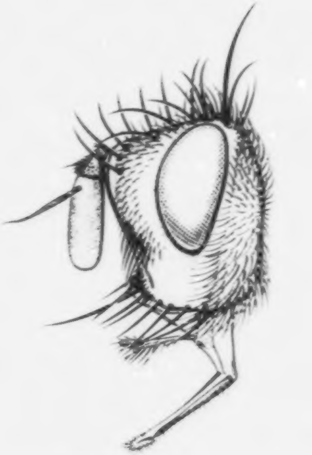
[40] Included in couplets 119–166 (except for *Eulasiona* (Dexiinae) and *Pelatachina* Meade (Tachininae)) are almost all the Nearctic genera of the tribe Blondeliini; generic synonymy is given by Wood (1985).



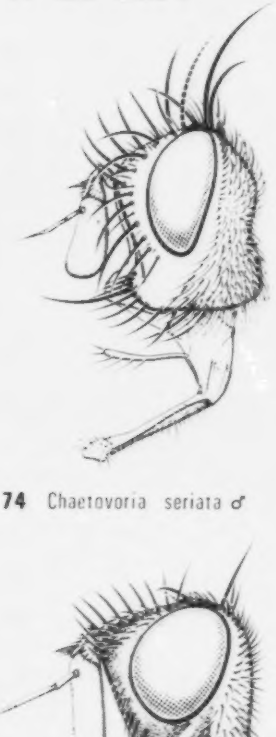
71 Voria ruralis ♂



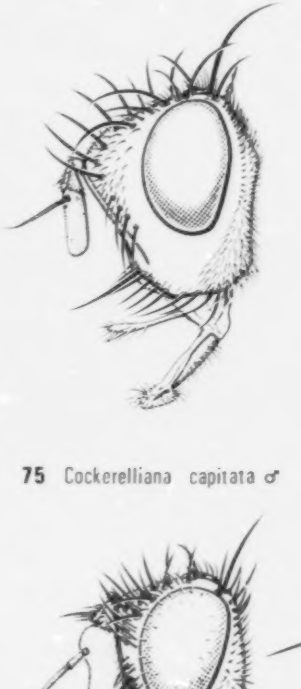
72 Cyrtophleba coquilletti ♂



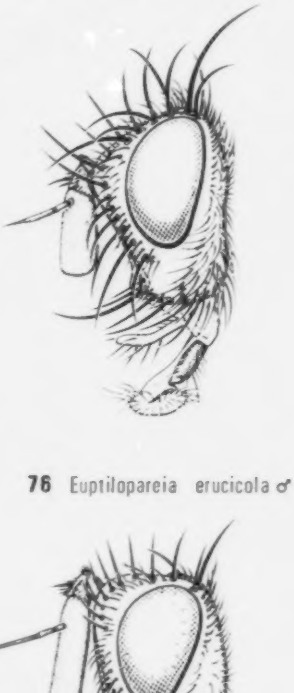
73 Menetus macropogon ♂



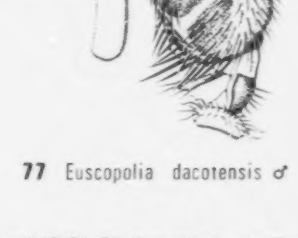
74 Chaetovoria seriata ♂



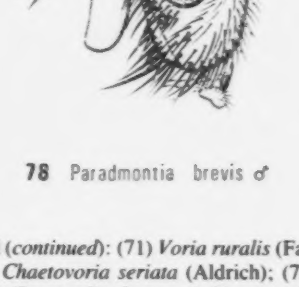
75 Cockerelliana capitata ♂



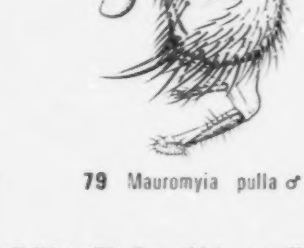
76 Euptilopareia erucicola ♂



77 Euscopolia dacotensis ♂

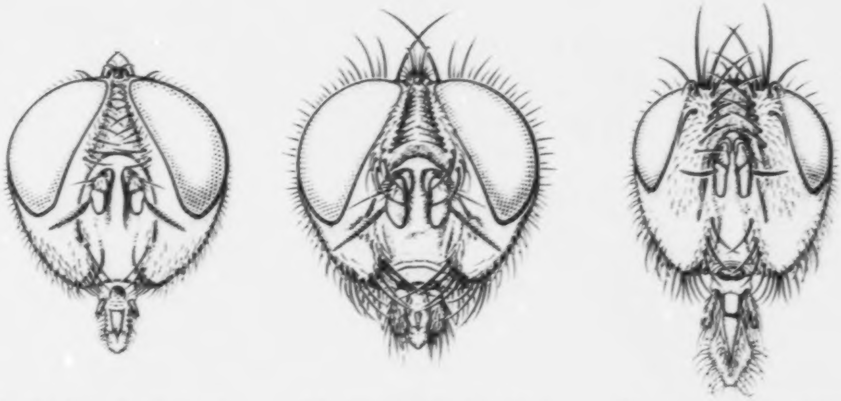


78 Paradmontia brevis ♂

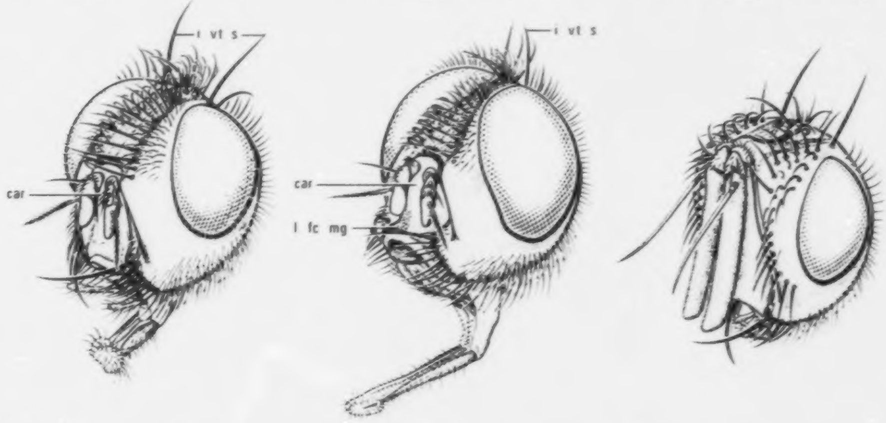


79 Mauromyia pulla ♂

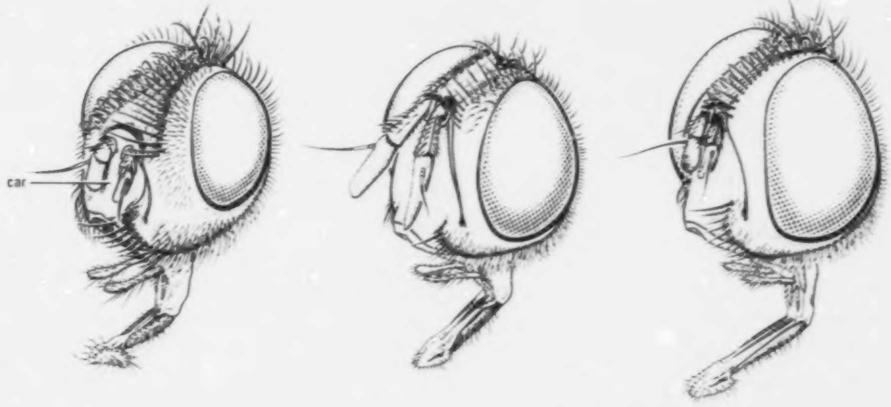
Figs. 110.71–79. Lateral views of head (*continued*): (71) *Voria ruralis* (Fallén); (72) *Cyrtophleba coquilletti* Aldrich; (73) *Menetus macropogon* (Bigot); (74) *Chaetovoria seriata* (Aldrich); (75) *Cockerelliana capitata* Townsend; (76) *Euptilopareia erucicola* (Coquillett); (77) *Euscopolia dacotensis* Townsend; (78) *Paradmontia brevis* Coquillett; (79) *Mauromyia pulla* Coquillett (*continued*).



80 Phasiops flavus ♂ **81** Eumegaparia flaveola ♂ **82** Microphthalma disjuncta ♀



83 Billaea satisfacta ♂ **84** Arctophyto marginalis ♂ **85** Hypertrophocera parvipes ♂



86 Ursophyto nigriceps ♂ **87** Gymnosoma canadensis ♀ **88** Gymnoclytia immaculata ♂

Figs. 110.80–88. Anterior views of head: anterior views of (80) *Phasiops flavus* Coquillett, (81) *Eumegaparia flaveola* (Coquillett), and (82) *Microphthalma disjuncta* (Wiedemann); oblique anterior views of (83) *Billaea satisfacta* (West), (84) *Arctophyto marginalis* Curran, (85) *Hypertrophocera parvipes* Townsend, (86) *Ursophyto nigriceps* (Bigot), (87) *Gymnosoma canadensis* (Brooks), and (88) *Gymnoclytia immaculata* (Macquart).

Abbreviations: car, carina; i vt s, inner vertical bristle; l fc mg, lower facial margin.

119. Middorsal depression on abdominal syntergite 1 + 2 extending back to hind margin of syntergite (Fig. 231) 120

Middorsal depression on abdominal syntergite 1 + 2 not extending back to hind margin of syntergite (Fig. 236) 123

120. Eye haired and facial ridge with bristles on lower two-thirds or more; ocellar bristles usually absent .... ***Compsilura*** Bouché, in part

1 introduced sp., *concinnata* (Meigen); widespread

Eye apparently bare, with hairs sparse and inconspicuous, if present; facial ridge usually without setae except on lowest fourth; ocellar bristles present, usually well-developed 121

121. Parafacial with decumbent hair on lower third to half, usually not extending up as high as lowest frontal bristle (Fig. 38). Parasites of sawfly larvae .... ***Vibrissina*** Rondani, in part

11 spp.; widespread; Aldrich 1931*a*, Reinhard 1958*a* (as *Spathimeigenia*)

Parafacial bare, except for a few hairs just below lowest frontal bristle. Parasites of larvae of Lepidoptera and larvae or adults of Coleoptera 122

122. Mid tibia with one anterodorsal bristle (a second, small bristle arising proximal to it) (as in Fig. 221) .... ***Eucelatoria*** Townsend, in part

10 spp.; widespread; Sabrosky 1981 (in part)

Mid tibia with at least three well-developed bristles, namely one or two small bristles above and one small one below largest bristle (as in Fig. 223) .... ***Blondelia*** Robineau-Desvoidy

6 spp.; widespread

123. Eye covered with conspicuous dense hairs; each hair longer than combined diameter of four or more eye facets (Figs. 37, 39, 41) 124

Eye apparently bare 132

124. Proepisternum setose (Fig. 166) .... ***Meigenia*** Robineau-Desvoidy

1 sp., *submissa* (Aldrich & Webber); western

Proepisternum bare (as in Figs. 167, 168) 125

125. Parafacial with hairs or bristles below lowest frontal bristle (Figs. 37, 39) 126

Parafacial bare 127

126. Facial ridge bristled on lower two-thirds or more; parafacial with small decumbent setae below lowest frontal bristle (Fig. 39) .... ***Istocheta*** Rondani

1 introduced sp., *aldrichi* (Mesnil); northeastern U.S.A.

Facial ridge bare or nearly so; parafacial with row or patch of long erect bristles (Fig. 37) .... ***Eulasiona*** Townsend, in part[41]

8 spp.; widespread; Curran 1927*b*

127. R_{4+5} setose nearly to crossvein r-m (as in Figs. 195, 199) .... ***Thelairodoria*** Townsend

1 sp., *setinervis* (Coquillett); eastern U.S.A.

R_{4+5} setose less than halfway to crossvein r-m 128

128. Male without proclinate orbital bristles. Female abdomen carinate midventrally and with sternite 7 modified into hook-like piercer (Fig. 256) 129

Male with proclinate orbital bristles. Female abdomen with a tubular or transversely flattened ovipositor (as in Figs. 258–260) 130

129. Facial ridge bristled on lower half or more (as in Fig. 39) .... ***Compsilura*** Bouché, in part

see couplet 120

Facial ridge bare except on lowest fourth or less (Fig. 38) .... ***Eucelatoria*** Townsend, in part

see couplet 122

130. Frons with three long slender upper orbital bristles, with the foremost proclinate and the hindmost lateroclinate (Fig. 51); lower facial margin strongly turned forward, projecting beyond vibrissal angles in lateral view (as in Fig. 11) .... ***Policheta*** Rondani

1 sp., *crassispinosa* Wood; Oregon

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[41] Also included are the species formerly included in *Canelomyia* Reinhard, *Lasionalia* Curran, *Paralispidea* Townsend, and *Paramuscopteryx* Townsend.

Frons with two stout upper orbital bristles, both of which proclinate (Fig. 41). Lower margin of face not protruding beyond vibrissal angles in lateral view 131

131. Body dark brown or black in ground color ....***Myiopharus*** Brauer & Bergenstamm, in part

14 spp.; widespread; Reinhard 1935, in part (as *Doryphorophaga*)

Body pale orange or yellow in ground color..........................***Angustia*** Sellers

1 sp., *angustivitta* (Aldrich & Webber); eastern U.S.A.

132. Subvibrissal ridge with a row of four or more well-developed bristles; this ridge longer than row of supravibrissal setae on facial ridge (Figs. 40, 142) 133

Subvibrissal ridge with at most three large bristles arranged in a row shorter than the row of setae above vibrissa 135

133. Ptilinal sulcus extending posteriorly below genal dilation to level of hind margin of eye; genal dilation somewhat triangular (Fig. 142). Abdominal syntergite 1 + 2 with more than one pair of median marginal bristles. Upper part of frons of female with lateroclinate upper orbital bristle arising outside of frontal row (as in Figs. 50, 51). Postpronotum with three basal bristles. Egg with thin white or transparent chorion ....***Pelatachina*** Meade

3 spp.; widespread

Ptilinal sulcus ending below vibrissa at level of front margin of eye; genal dilation scarcely developed (Fig. 40). Abdominal syntergite 1 + 2 with only one pair of median marginal bristles. Frons of female lacking a lateroclinate bristle. Postpronotum usually with only two large basal bristles, namely the outer and middle basal bristles; inner bristle usually hair-like (as in Fig. 156). Egg planoconvex, with tough pale brown shiny chorion and thickened edges 134

134. Parafacial with hairs, at least on upper two-thirds or more (hairs sometimes pale, concolorous with parafacial and thus visible only against a dark background) (Fig. 40)............ ....***Cryptomeigenia*** Brauer & Bergenstamm

14 spp.; widespread; Curran 1926

Parafacial bare, or with a few hairs on upper third below lowest frontal bristle (as in Fig. 48) ....***Zaira*** Robineau-Desvoidy

13 spp.; widespread; Reinhard 1930*a* (as *Viviania*)

135. Male with two pairs of slender proclinate orbital bristles crowded against frontal bristles on narrow frons (Fig. 53). Sternite 5 of male usually with pair of tufts of curved setae. Female with broad ovipositor, flattened dorsoventrally; sternite 7 truncate or obtusely pointed; midventral margins of some abdominal tergites with paired patches of thorn-like bristles (Fig. 252). Posteroapical margin of hind coxa with similar bristles.....***Medina*** Robineau-Desvoidy

4 spp.; widespread

Male with much broader frons, with or without proclinate orbital bristles. Sternite 5 of male without tufts of curved setae. Female with tubular ovipositor or with saber-like piercer 136

136. Eye almost as high as head; gena in lateral view reduced to a narrow setose strip less than one-tenth height of head (as in Fig. 99) 137

Eye height much less than head height; gena at least one-sixth height of head 138

137. Ocellar setae arising beside or in front of anterior ocellus; fronto-orbital plate with row of four or more proclinate orbital bristles (Fig. 52) ....***Euhalidaya*** Walton, in part

1 sp., *genalis* (Coquillett); widespread

Ocellar setae arising behind anterior ocellus; fronto-orbital plate with two or three proclinate orbital bristles ....***Sphaerina*** Wulp

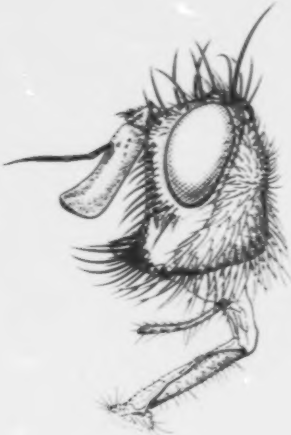
1 sp., *linearis* (Townsend); southern Florida

138. Facial ridge setose on lower half or more (Figs. 42–45) 139

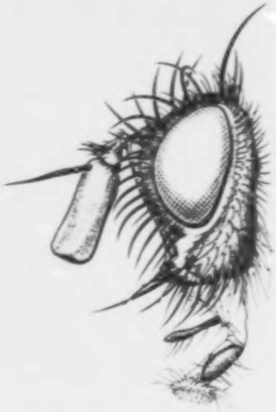
Facial ridge bare except on lowest one third or less 147

139. Scape, pedicel, and first flagellomere bright orange; arista of male usually thickened to apex (Fig. 128). Facial ridge prominent in lateral view, appearing as a band anterior to parafacial, and usually adorned with small scattered setae on lower half or more. Parasite of the walkingstick ....***Phasmophaga*** Townsend, in part

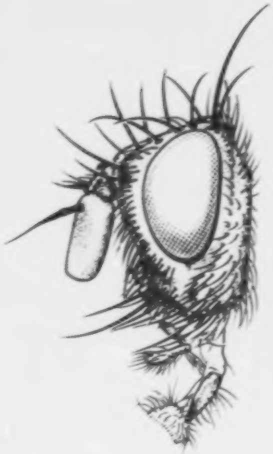
4 spp.; eastern U.S.A. and southern Canada



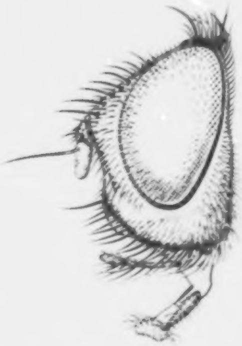
89 Periscepsia stylata ♂



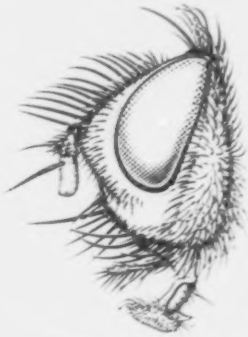
90 Periscepsia helymus ♂



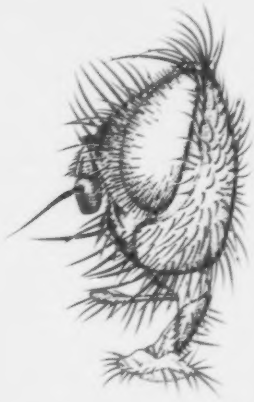
91 Goniocera io ♂



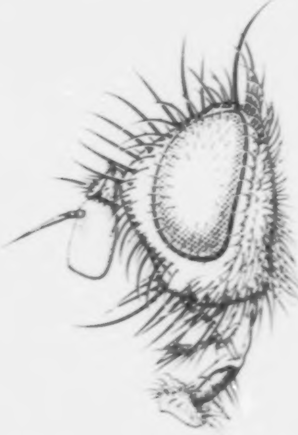
92 Gnadochaeta clistoides ♂



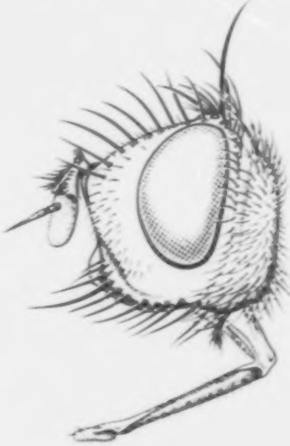
93 Phyllomya washingtoniana ♂



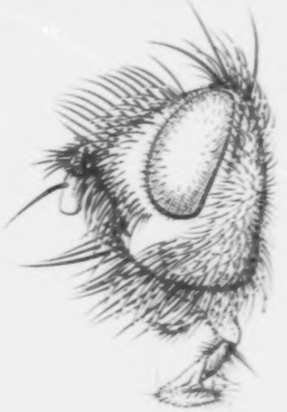
94 Macquartia obscura ♂



95 Blepharomyia tibialis ♂

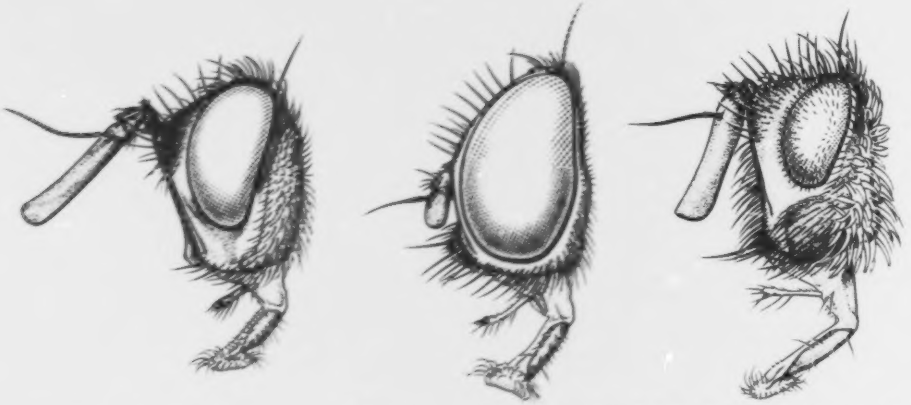


96 Meledonus latipennis ♂

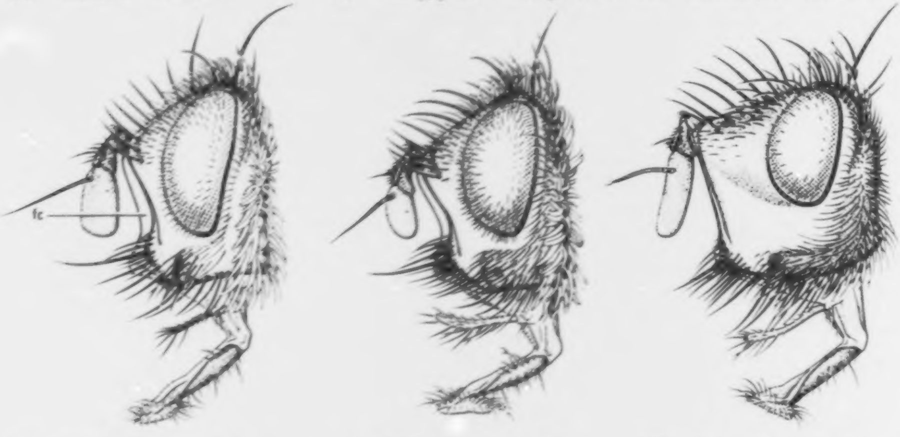


97 Metopomuscopteryx tibialis ♂

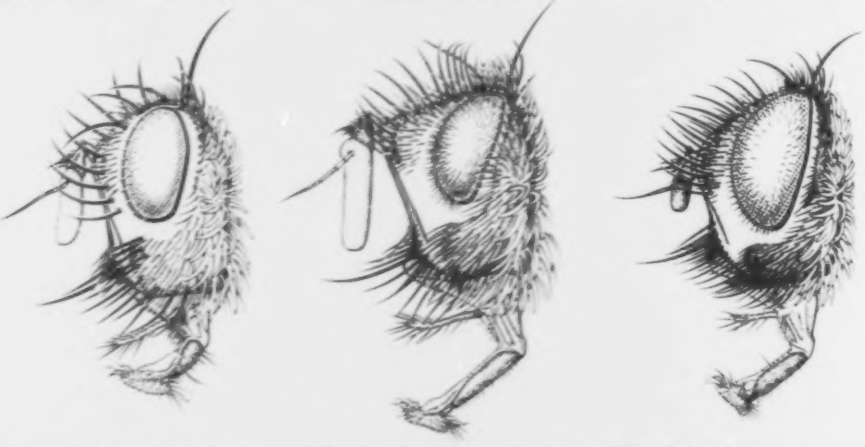
Figs. 110.89–97. Lateral views of head (*continued*): (89) *Periscepsia stylata* (Brauer & Bergenstamm); (90) *Periscepsia helymus* (Walker); (91) *Goniocera io* (Aldrich); (92) *Gnadochaeta clistoides* (Townsend); (93) *Phyllomya washingtoniana* (Bigot); (94) *Macquartia obscura* (Coquillett); (95) *Blepharomyia tibialis* (Curran); (96) *Meledonus latipennis* Aldrich; (97) *Metopomuscopteryx tibialis* (Coquillett) (*continued*).



98 Penthosia satanica ♂ **99** Strongygaster triangulifera ♀ **100** Mactomyia fracida ♂



101 Linnaemya tessellata ♂ **102** Panzeria ampelus ♂ **103** Melanophrys flavipennis ♂



104 Dichocera robusta ♀ **105** Ostracophyto aristalis ♂ **106** Spilochaetosoma californicum ♂

Figs. 110.98–106. Lateral views of head (*continued*): (98) *Penthosia satanica* (Bigot); (99) *Strongygaster triangulifera* (Loew); (100) *Mactomyia fracida* Reinhard; (101) *Linnaemya tessellata* (Brooks); (102) *Panzeria ampelus* (Walker); (103) *Melanophrys flavipennis* Williston; (104) *Dichocera robusta* Brooks; (105) *Ostracophyto aristalis* Townsend; (106) *Spilochaetosoma californicum* Smith (*continued*).

Abbreviation: fc, face.

Antenna usually black (partially orange in *Admontia nasoni* Coquillett, with row of small bristles on parafacial); arista hair-like on apical third or more. Facial ridge usually not prominent in lateral view except for that portion just above vibrissa. Parasite of insects other than the walkingstick 140

140. Parafacial with a patch of small setae adjacent to ptilinal suture and usually continuous with small setae outside lower frontal bristles; setae usually extending ventrally at least to a level opposite uppermost bristles on facial ridge (Fig. 42) .... **Admontia** Brauer & Bergenstamm

10 spp.; widespread; Curran 1927*a*

Parafacial without setae below lowest frontal bristle 141

141. Base of R_{4+5} with a single long seta, usually as long as a third or more the distance to cross-vein r-m (as in Figs. 193, 196). Parafacial narrow and parallel-sided (Fig. 43). Sternite 7 of female forming an enormous sickle-shaped piercer, opposing a seta-studded peg-like extension of ventral margin of syntergite 1 + 2 (Fig. 257) .... **Celatoria** Coquillett

2 spp.; widespread

Base of R_{4+5} usually with two or more shorter setae. Parafacial, if narrow, not parallel-sided, instead tapering ventrally. Piercer, if present (as in *Chaetonodexodes*), inconspicuous, often concealed between ventral margins of tergites 142

142. Discal bristles absent on abdominal tergite 3. Median marginal bristles on tergite 3 arising rather far forward, halfway between middle and hind margin of tergite (Fig. 236). Female with small hooked piercer .... **Chaetonodexodes** Townsend, in part

1 sp., *vanderwulpi* (Townsend); southern; Aldrich 1931*b*

Discal bristles present on abdominal tergite 3 (as in Fig. 231). Median marginal bristles on tergite 3 arising closer to hind margin of tergite than to middle. Female without piercer . . . 143

143. Setae on facial ridge decreasing markedly in length and thickness dorsally, becoming hair-like above lower fourth (Fig. 44) .... **Eribella** Mesnil

2 spp.; widespread

Setae on facial ridge decreasing only slightly in length and thickness dorsally, retaining their bristle-like appearance nearly to the uppermost seta (Fig. 45) 144

144. Katepisternum with two bristles. Male with only one stout proclinate upper orbital bristle (Fig. 45) .... **Anoxynops** Townsend

1 sp., *aldrichi* (Curran); eastern, southwestern

Katepisternum with three bristles. Male without or with two proclinate upper orbital bristles (Fig. 41) 145

145. M ending in R_{4+5} well before wing margin (as in Fig. 191) . . . **Ligeria** Robineau-Desvoidy

1 sp., *latigena* Wood; Arctic

M ending in wing margin 146

146. Middle katepisternal bristle arising close to anterior bristle, three times farther from posterior katepisternal as from anterior katepisternal (Fig. 173) .... **Myiopharus** Brauer & Bergenstamm, in part

see couplet 130

Middle katepisternal bristle about equidistant between anterior katepisternal and posterior katepisternal bristles .... **Oxynops** Townsend

1 sp., *anthracinus* (Bigot); widespread

147. Lateral scutellar bristle absent (Fig. 186) 148

Lateral scutellar bristle present (Figs. 184, 185) 150

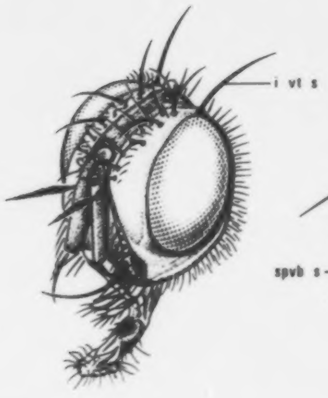
148. Vibrissa arising from anteroventral corner of head, without any subvibrissal bristles arising ventral to it (Fig. 46). Abdominal sternite 7 of female in the form of a small piercer ensheathed in scoop-like sternite 6 (Fig. 258) .... **Phyllophilopsis** Townsend, in part

2 spp.; eastern

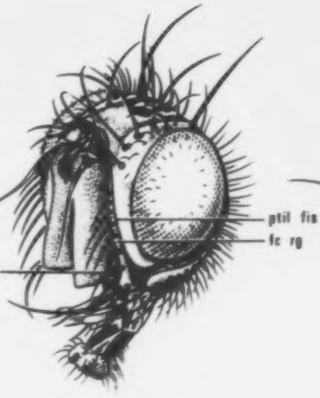
Vibrissa with one or more subvibrissal bristles ventral to it (as in Figs. 43, 44). Female with tubular telescopic ovipositor without piercer (Figs. 259, 260) 149

149. M ending in R_{4+5} well before wing margin (as in Fig. 191). Female abdomen globular (as in Fig. 260) .... **Steleoneura** Stein

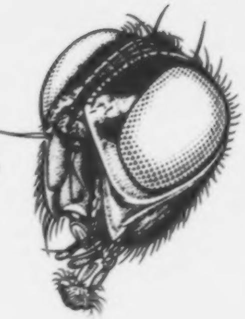
1 sp., *novemmaculata* Wood; northwestern Arctic



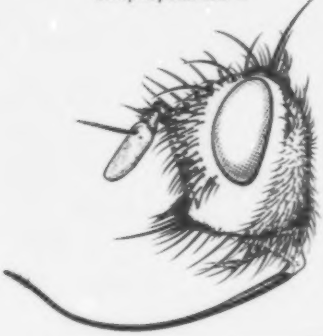
107 Vanderwulpia atrophopodoides ♂



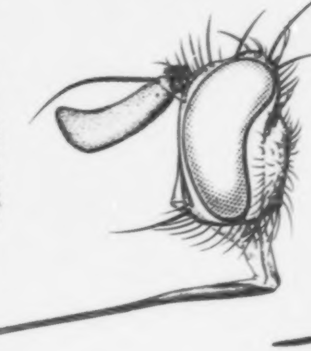
108 Campylochaeta semiothisae ♂



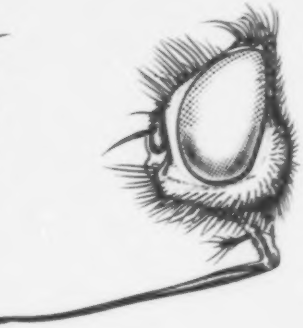
109 Bezzimyia sp. ♂



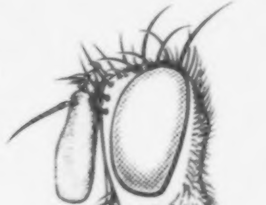
110 Trochilodes skinneri ♂



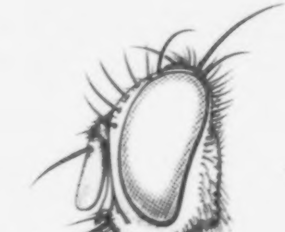
111 Beskia aelops ♂



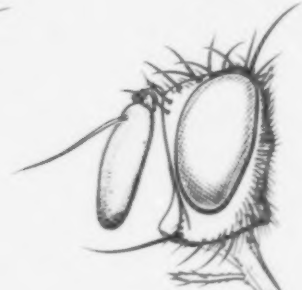
112 Imitomyia sugens ♂



113 Clausicella politura ♂



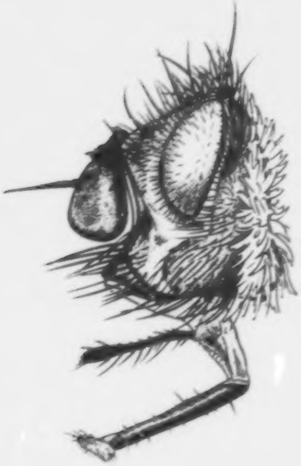
114 Epigrimyia polita ♂



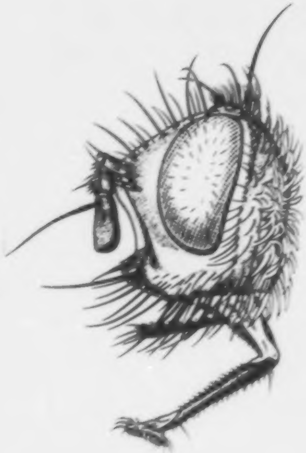
115 Crocinosoma cornuale ♀

Figs. 110.107–115. Anterolateral and lateral (*continued*) views of head: anterolateral views of (107) *Vanderwulpia atrophopodoides* Townsend, (108) *Campylochaeta semiothisae* (Brooks), and (109) *Bezzimyia* sp.; lateral views of (110) *Trochilodes skinneri* Coquillett, (111) *Beskia aelops* (Walker), (112) *Imitomyia sugens* (Loew), (113) *Clausicella politura* (Reinhard), (114) *Epigrimyia polita* Townsend, and (115) *Crocinosoma cornuale* Reinhard (*continued*).

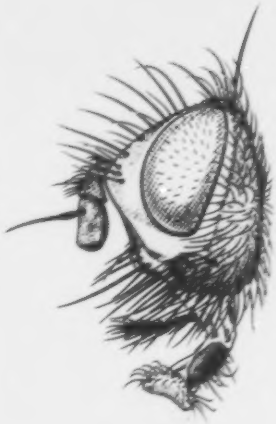
Abbreviations: i vt s, inner vertical seta; fc rg, facial ridge; ptil fis, ptilinal fissure; spvb s, supravibrissal bristle.



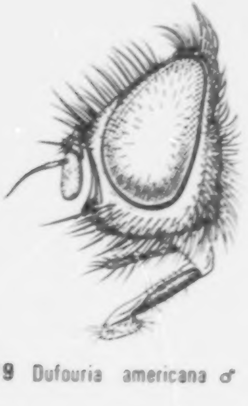
116 Trafoia arctica ♂



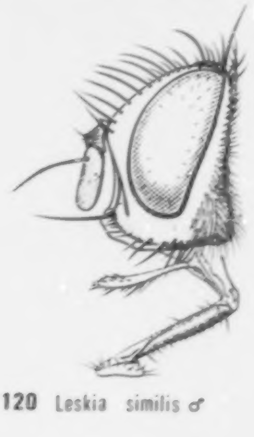
117 Eriothrix penitalis ♂



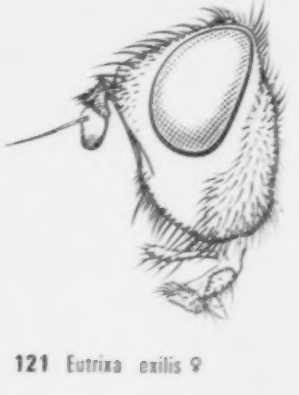
118 Cleonice bigelowi ♂



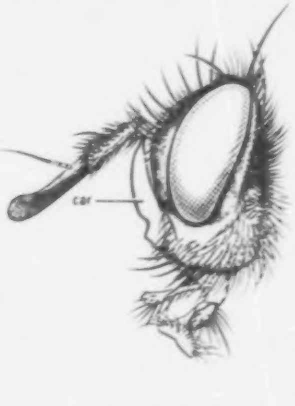
119 Dufouria americana ♂



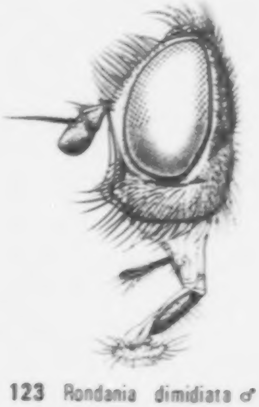
120 Leskia similis ♂



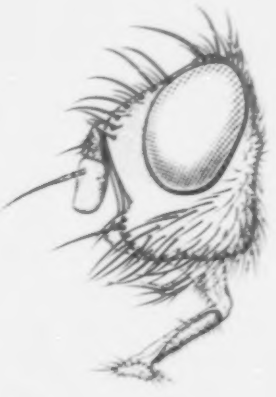
121 Eutrixa exilis ♀



122 Euthera tentatrix ♂



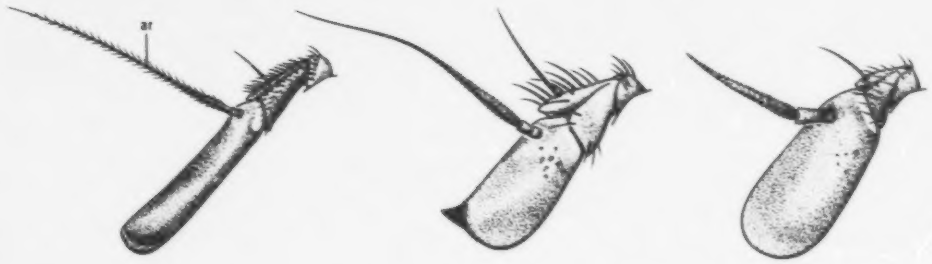
123 Rondania dimidiata ♂



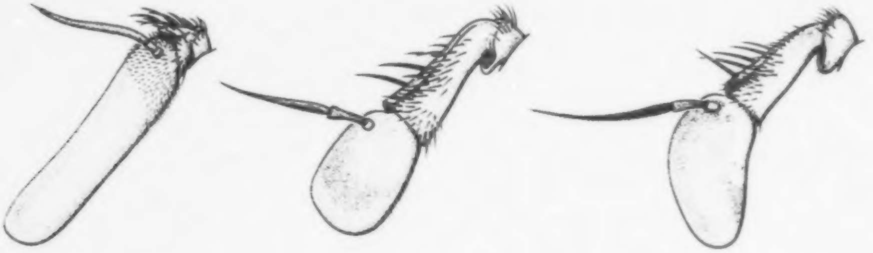
124 Clastoneuriopsis meralis ♂

Figs. 110.116–124. Lateral views of head (*concluded*): (116) *Trafoia arctica* (Sack); (117) *Eriothrix penitalis* (Coquillett); (118) *Cleonice bigelowi* (Curran); (119) *Dufouria americana* Reinhard; (120) *Leskia similis* (Townsend); (121) *Eutrixa exilis* (Coquillett); (122) *Euthera tentatrix* Loew; (123) *Rondania dimidiata* (Meigen); (124) *Clastoneuriopsis meralis* Reinhard.

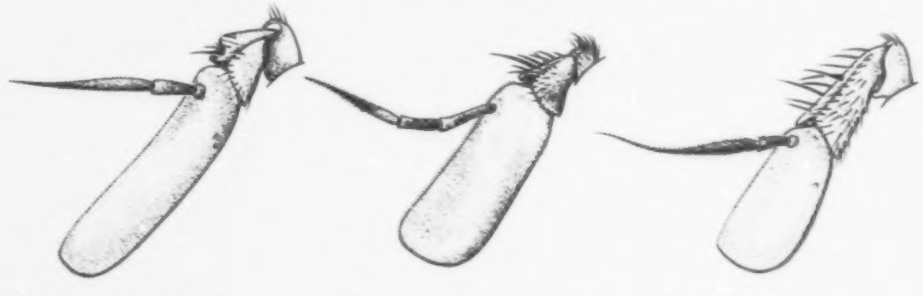
Abbreviation: car, carina.



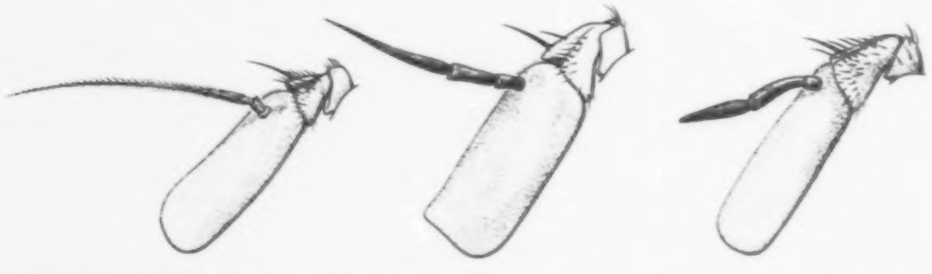
125 Prospherysa pulverea ♀ **126** Ceracia dentata ♂ **127** Evidomyia infida ♂



128 Phasmophaga antennalis ♂ **129** Tachina florum ♂ **130** Archytas apicifer ♂

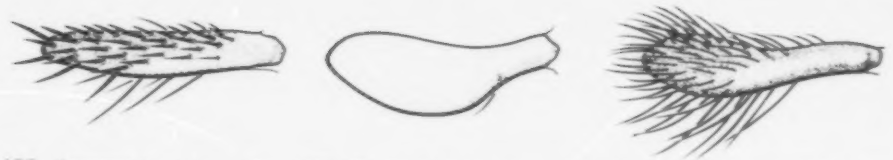


131 Psilopleura arida ♀ **132** Triarthria spinipennis ♂ **133** Aphria ocypterata ♂

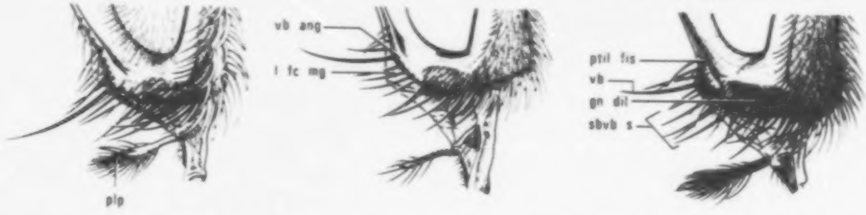


134 Genea robertsonii ♂ **135** Impeccantia claterna ♂ **136** Germaria sp. ♂

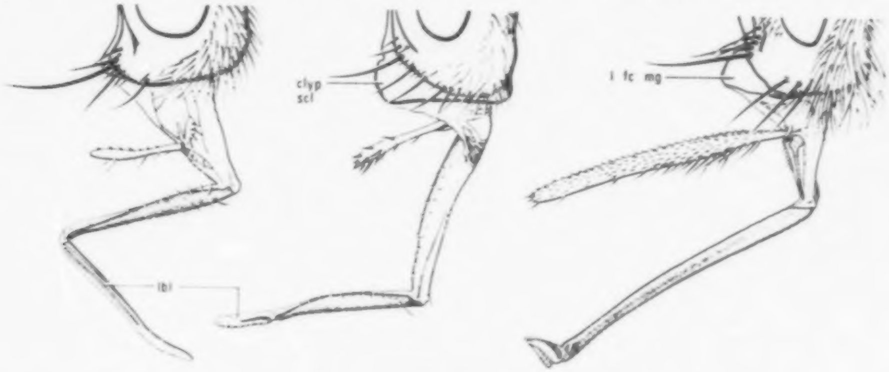
Figs. 110.125–136. Lateral views of left antenna: (125) *Prospherysa pulverea* (Coquillett); (126) *Ceracia dentata* (Coquillett); (127) *Evidomyia infida* Reinhard; (128) *Phasmophaga antennalis* Townsend; (129) *Tachina florum* Walker; (130) *Archytas apicifer* (Walker); (131) *Psilopleura arida* Reinhard; (132) *Triarthria spinipennis* (Meigen); (133) *Aphria ocypterata* Townsend; (134) *Genea robertsonii* (Townsend); (135) *Impeccantia claterna* Reinhard; (136) *Germaria* sp. Abbreviation: ar, arista.



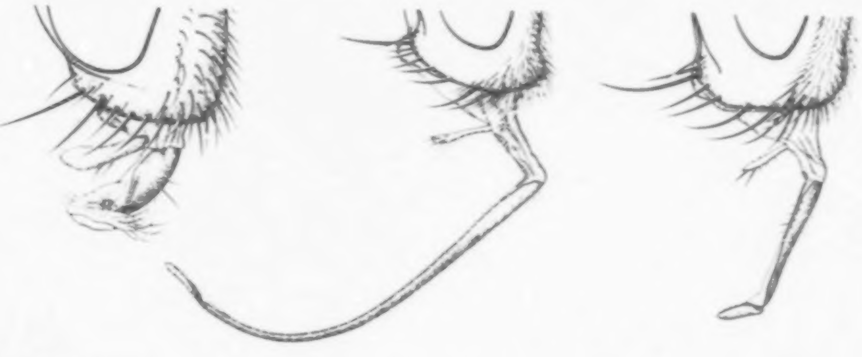
137 Euceromasia spinosa ♀ **138** Hypertrophomma opaca ♀ **139** Eumasicera coccidella ♂



140 Myxexoristops fronto ♂ **141** Masiphya confusa ♂ **142** Pelatachina pellucida ♂



143 Siphona intrudens ♂ **144** Ginglymia acrirostris ♀ **145** Adejeania vexatrix ♂



146 Anthomyiopsis cypseloides ♀ **147** Prosenoides flavipes ♂ **148** Plagiomima similis ♂

Figs. 110.137–148. Palpi and heads: lateral views of left palpus of (137) *Euceromasia spinosa* Townsend, (138) *Hypertrophomma opaca* Townsend, and (139) *Eumasicera coccidella* Townsend; lateral views of ventral part of head of (140) *Myxexoristops fronto* (Coquillett), (141) *Masiphya confusa* Aldrich, (142) *Pelatachina pellucida* Coquillett, (143) *Siphona intrudens* (Curran), (144) *Ginglymia acrirostris* Townsend, (145) *Adejeania vexatrix* (Osten Sacken), (146) *Anthomyiopsis cypseloides* Townsend, (147) *Prosenoides flavipes* Coquillett, and (148) *Plagiomima similis* (Townsend).

Abbreviations: clyp scl, clypeal sclerite; gn dil, genal dilation; lbl, labella; l fc mg, lower facial margin; plp, palpus; ptil fis, ptilinal fissure; sbvb s, subvibrissal bristle; vb, vibrissa; vb ang, vibrissal angle.

M ending in r_{4+5} at wing margin or ending separately from R_{4+5} (as in Fig. 193). Female abdomen somewhat flattened from side to side (Fig. 259) .... ***Dolichotarsus*** Brooks, in part
4 spp.; widespread

150. Discal bristles absent on abdominal tergites 3 and 4 151
Discal bristles present on abdominal tergites 3 and 4 152

151. M and R_{4+5} each ending separately rather far apart on either side of wing apex (Fig. 195) or M ending in membrane at point where bend should be, as in *C. manca* (Greene) .... ***Chaetostigmoptera*** Townsend
4 spp.; widespread
M and R_{4+5} both ending anterior to wing apex (as in Fig. 193) .... ***Myiopharus*** Brauer & Bergenstamm, in part
see couplet 131

152. Parafacial with setae extending from lowest frontal at least to middle of parafacial (Fig. 37) 153
Parafacial bare except for an occasional hair just below lowest frontal bristle (as in Figs. 35, 36) 156

153. Parafacial with a row of rather regularly arranged erect bristles (Fig. 37). Median marginal bristles on abdominal tergites 3 and 4 arising nearer middle than posterior margin of tergite .... ***Eulasiona*** Townsend, in part
see couplet 126
Parafacial with scattered setae (Fig. 47). Median marginal bristles arising nearer posterior margin than middle of tergites 3 and 4 154

154. Occiput without genal dilation; genal groove extensive (Fig. 47) ...... ***Enrogalia*** Reinhard
1 sp., *morigera* Reinhard; California
Occiput with a small but distinct genal dilation and correspondingly reduced genal groove 155

155. M ending in R_{4+5} well before wing margin (as in Fig. 191) .... ***Erynniopsis*** Townsend
1 introduced sp., *antennata* (Rondani); California
M ending in wing margin .... ***Lixophaga*** Townsend, in part
16 spp.; widespread; Aldrich 1925*a*, Curran 1935

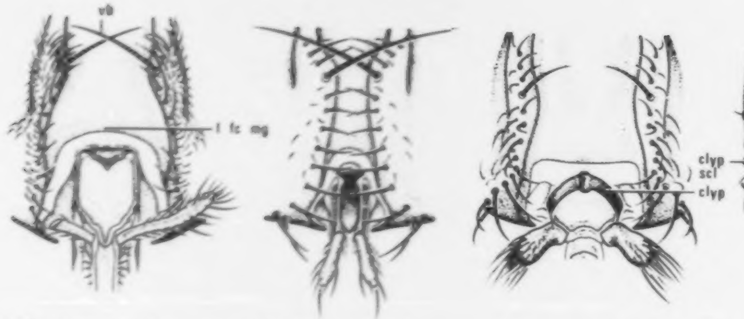
156. Postpronotum with two bristles, or with three arranged in a nearly straight row (as in Figs. 156, 158) 157
Postpronotum with at least three bristles, arranged in a triangle (Figs. 157, 159) 159

157. Occiput with a genal dilation (as in Fig. 41) .... ***Meigenielloides*** Townsend
1 sp., *cinerea* Townsend; western
Occiput without a genal dilation (as in Figs. 47, 48) 158

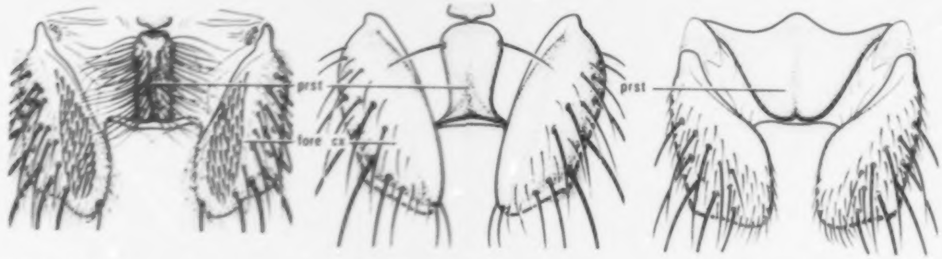
158. Both sexes with three upper orbital bristles, two of which are proclinate and the posteriormost one lateroclinate (Fig. 48). Parafacial very wide; eye small and rounded. Sternite 7 of female folded longitudinally .... ***Picconia*** Robineau-Desvoidy
1 sp., *derisa* (Reinhard); widespread
Neither sex with a lateroclinate upper orbital bristle. Parafacial narrower; eye more elliptic. Sternite 7 of female simple, unfolded .... ***Anisia*** Wulp, in part
4 spp.; widespread; Reinhard 1942*b* (as *Oedematocera*)

159. Proepisternum with a small patch of hairs (as in Fig. 166) .... ***Prodegeeria*** Brauer & Bergenstamm
3 spp.; widespread
Proepisternum bare (a single hair may rarely be present in *Belida*) 160

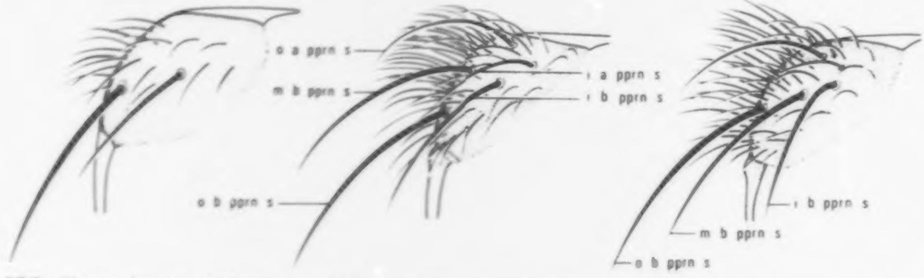
160. Abdominal tergites 3 and 4 each with two or more pairs of discal bristles; the median pair arising at most slightly anterior to lateral ones (Fig. 237) 161
If abdominal tergites 3 and 4 with two pairs of discal bristles, then one pair decidedly anterior to other pair (as in Fig. 239) 162



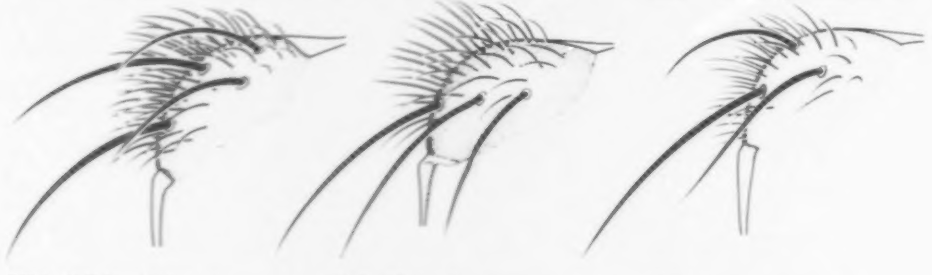
149 Mystacomyia scordala ♂ **150** Megapariopsis opaca ♀ **151** Eumegaparia flaveola ♂ **152** Clausicella politura ♀



153 Macromya crocata ♂ **154** Microchaetina valida ♂ **155** Ormia dominicana ♂



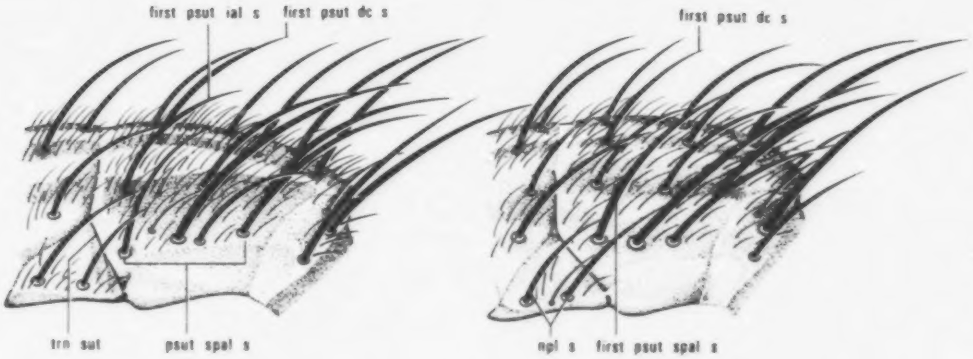
156 Chaetoglossa picticornis ♂ **157** Patelloa leucaniae ♂ **158** Phryxe pecosensis ♂



159 Belida dexina ♂ **160** Wagneria vernata ♂ **161** Genea tenera ♂

Figs. 110.149–161. Faces, prosterna, and postpronota: anterior views of lower facial margin and clypeus of (149) *Mystacomyia scordala* (Reinhard), (150) *Megapariopsis opaca* (Coquillett), (151) *Eumegaparia flaveola* (Coquillett), and (152) *Clausicella politura* (Reinhard); anteroventral views of prosternum and fore coxa of (153) *Macromya crocata* Reinhard, (154) *Microchaetina valida* (Townsend), and (155) *Ormia dominicana* Townsend; dorsal views of left postpronotum of (156) *Chaetoglossa picticornis* Townsend, (157) *Patelloa leucaniae* (Coquillett), (158) *Phryxe pecosensis* (Townsend), (159) *Belida dexina* (Townsend), (160) *Wagneria vernata* West, and (161) *Genea tenera* (Wiedemann).

Abbreviations: a, anterior; b, basal; clyp, clypeus; clyp scl, clypeal sclerite; fore cx, fore coxa; i, inner; l fc mg, lower facial margin; m, middle; o, outer; pprn, postpronotal; prst, prosternum; s, bristle; vb, vibrissa.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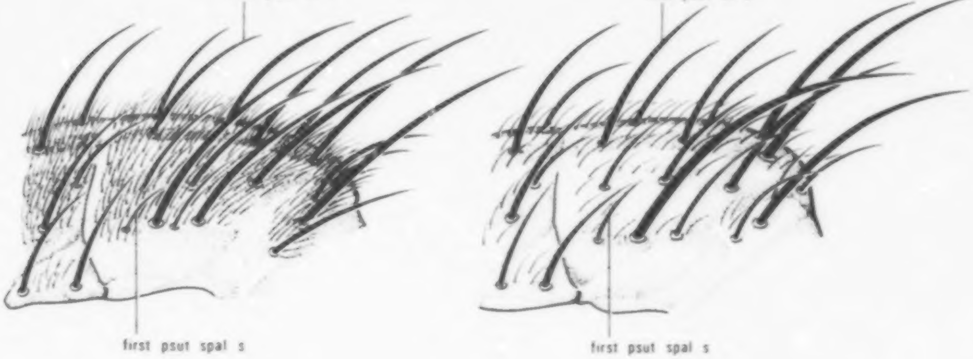
162 Xanthophyto labis ♀ **163** Atactopsis reinhardi ♀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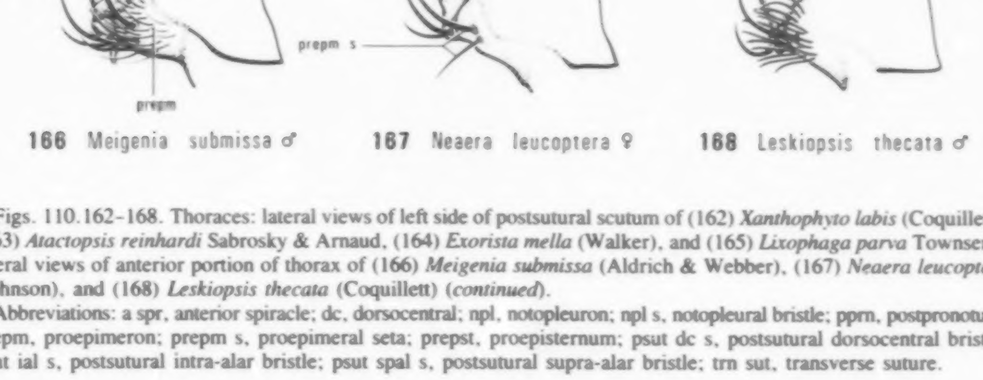
164 Exorista mella ♂ **165** Lixophaga parva ♂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166 Meigenia submissa ♂ **167** Neaera leucoptera ♀ **168** Leskiopsis thecata ♂

Figs. 110.162–168. Thoraces: lateral views of left side of postsutural scutum of (162) *Xanthophyto labis* (Coquillett), (163) *Atactopsis reinhardi* Sabrosky & Arnaud, (164) *Exorista mella* (Walker), and (165) *Lixophaga parva* Townsend; lateral views of anterior portion of thorax of (166) *Meigenia submissa* (Aldrich & Webber), (167) *Neaera leucoptera* (Johnson), and (168) *Leskiopsis thecata* (Coquillett) (*continued*).

Abbreviations: a spr, anterior spiracle; dc, dorsocentral; npl, notopleuron; npl s, notopleural bristle; pprn, postpronotum; prepm, proepimeron; prepm s, proepimeral seta; prepst, proepisternum; psut dc s, postsutural dorsocentral bristle; psut ial s, postsutural intra-alar bristle; psut spal s, postsutural supra-alar bristle; trn sut, transverse suture.

161. Mid tibia with two anterodorsal bristles (Fig. 222) .... ***Oswaldia*** Robineau-Desvoidy
9 spp.; widespread

Mid tibia with one anterodorsal bristle (as in Fig. 221) .... ***Opsomeigenia*** Townsend, in part
7 spp.; widespread

162. Lateral scutellar bristles as long and straight as subapical scutellar bristles (Fig. 185); prosternum with white hairs. Abdomen of female with well-developed midventral carina; ventral margin of tergite 4 with short stout bristles .... ***Eucelatoria*** Townsend, in part
see couplet 122

Lateral scutellar bristles two-thirds as long as subapical bristles (as in Fig. 184); prosternum with black hairs. Abdomen of female with well-developed midventral carina only in some species of *Vibrissina*, in which margins of both tergites 3 and 4 are armed with stout bristles 163

163. Postpronotum with four bristles arranged in a parallelogram, with the middle basal one displaced anteriorly (Fig. 159) .... ***Belida*** Robineau-Desvoidy
3 spp.; widespread

Postpronotum usually with three bristles, but if with four, then the three basal bristles arranged in a straight line (as in Fig. 158) 164

164. Parafacial strongly narrowed ventrally (Fig. 49). Abdomen of female strongly bent ventrally, with a telescopic tubular ovipositor directed ventrally (as in Fig. 260) .... ***Trigonospila*** Pokorny, in part
3 spp.; eastern U.S.A., Mexico

Parafacial not as strongly narrowed ventrally (Fig. 38). Ovipositor, if telescopic, not directed ventrally 165

165. Katepisternum with two bristles (as in Fig. 172). Abdomen of female with midventral carina; sternite 7 modified into a hook-like piercer (shorter than that in Fig. 256) .... ***Vibrissina*** Rondani, in part
see couplet 121

Katepisternum with three bristles. Abdomen of female with neither midventral carina nor piercer 166

166. Scutum with three pairs of presutural acrostichal bristles. Sternite 5 of male with a single long bristle (Fig. 262); sternites 5 and 6 of female rounded or truncate apically .... ***Lixophaga*** Townsend, in part
see couplet 155

Scutum with only two pairs of presutural acrostichal bristles, the anterior two pairs present, the posteriormost pair absent. Sternite 5 of male lacking a long bristle; sternites 5 and 6 of female large, heavily sclerotized, pointed apically (as in Fig. 258) .... ***Calolydella*** Townsend
2 spp.; southwestern and eastern

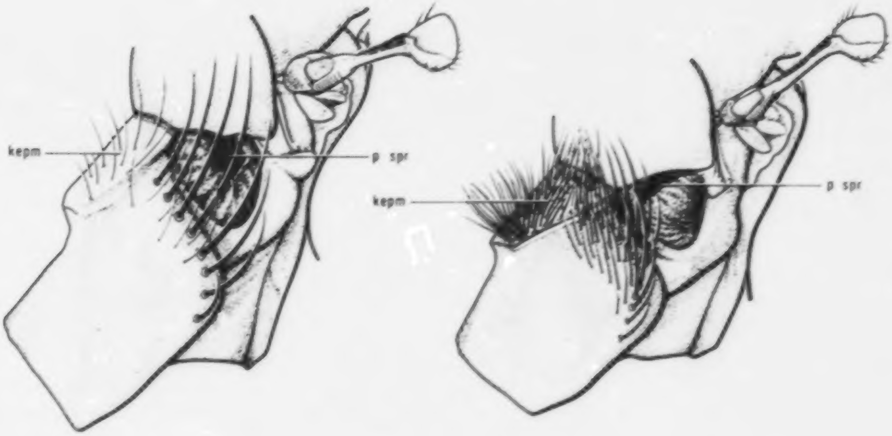
167. A_1 ending at wing margin (Fig. 199). Lower katepisternal bristle usually larger than anterodorsal katepisternal bristle 168

A_1 ending in membrane, before reaching margin. Lower katepisternal bristle usually smaller than anterodorsal katepisternal bristle 170

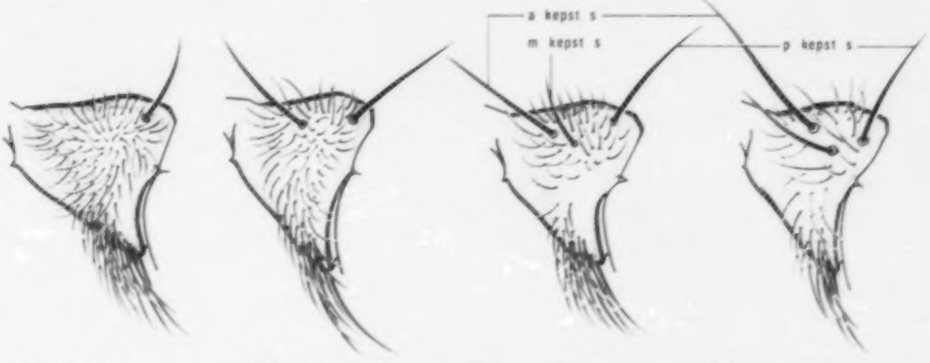
168. Proboscis elongate; labella usually as long as mentum (Fig. 143) .... ***Siphona*** Meigen
14 spp.; widespread; Curran 1932, O'Hara 1982

Proboscis shorter; labella much shorter than mentum (as in Fig. 144) 169

169. Mid tibia without anterodorsal bristle. Lower katepimeral bristle smaller than anterodorsal bristle. First aristomere 2 or more times as long as wide; third aristomere rather short, about 1.5 times as long as combined length of first and second aristomeres .... ***Baeomyia*** O'Hara
5 spp.; western; O'Hara 1984


kepm
p spr
kepm
p spr

169 Chrysotachina alcedo ♂ **170** Winthemia fumiferanae ♂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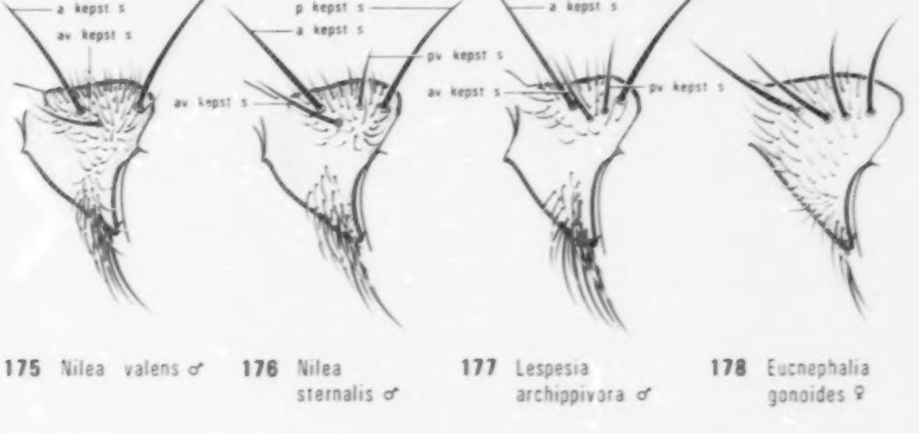
171 Phasia diversa ♂ **172** Anoxynops aldrichi ♂ **173** Myiopharus dorsalis ♂ **174** Phryxe pecosensis ♂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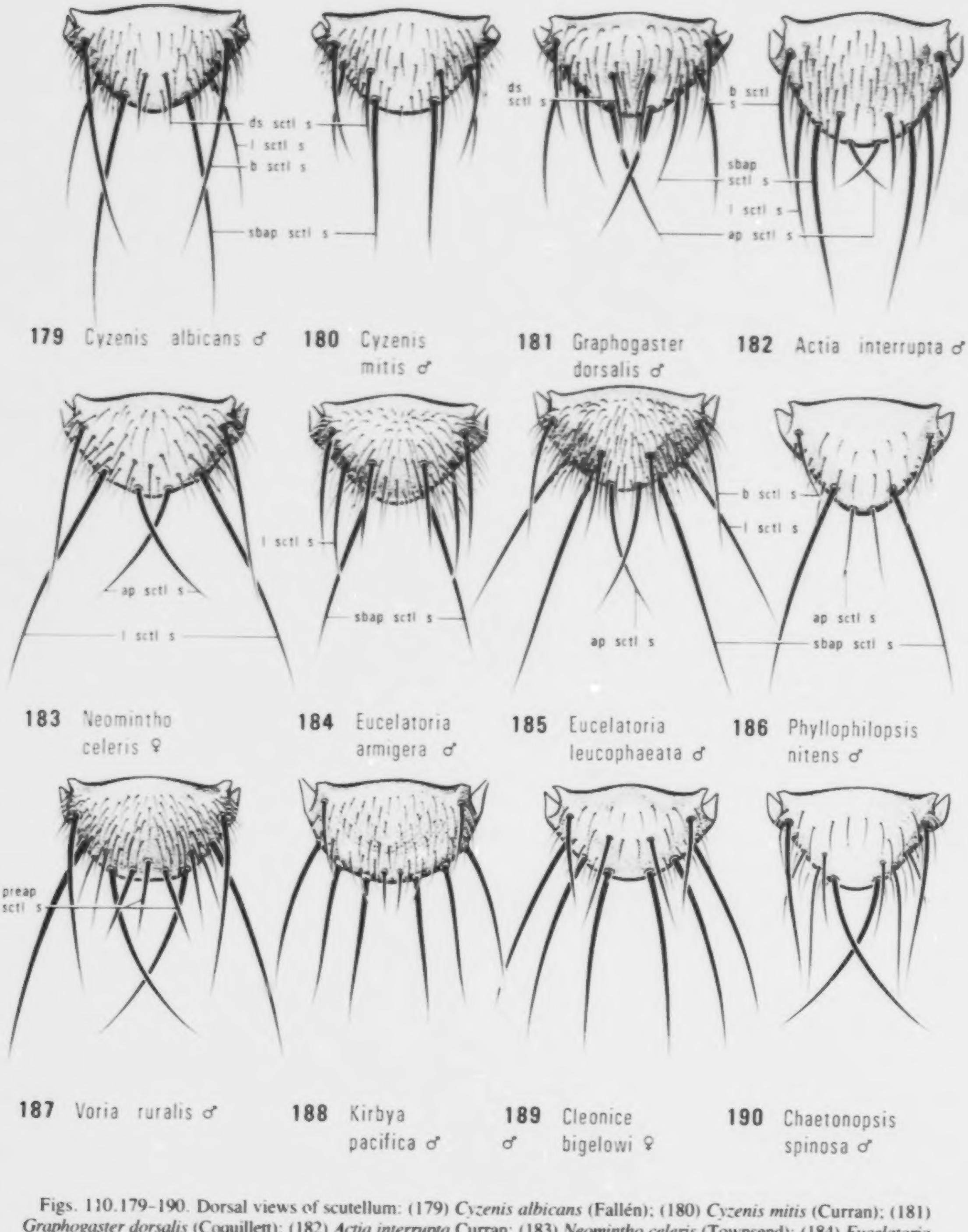
175 Nilea valens ♂ **176** Nilea sternalis ♂ **177** Lespesia archippivora ♂ **178** Eucnephalia gonoides ♀

Figs. 110. 169–178. Thoraces (*concluded*): lateral views of katepimeron and posterior spiracle of (169) *Chrysotachina alcedo* (Loew) and (170) *Winthemia fumiferanae* Tothill; lateral views of left katepisternum of (171) *Phasia diversa* (Coquillett), (172) *Anoxynops aldrichi* (Curran), (173) *Myiopharus dorsalis* (Coquillett), (174) *Phryxe pecosensis* (Townsend), (175) *Nilea valens* (Aldrich & Webber), (176) *Nilea sternalis* (Coquillett), (177) *Lespesia archippivora* (Riley), and (178) *Eucnephalia gonoides* Townsend.

Abbreviations: a, anterior; av, anteroventral; kepm, katepimeron; kepst s, katepisternal bristle; m, middle; p, posterior; p spr, posterior spiracle; pv, posteroventral.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sbap sctl s
preap sctl s

179 Cyzenis albicans ♂

180 Cyzenis mitis ♂

181 Graphogaster dorsalis ♂

182 Actia interrupta ♂

183 Neomintho celeris ♀

184 Eucelatoria armigera ♂

185 Eucelatoria leucophaeata ♂

186 Phyllophilopsis nitens ♂

187 Voria ruralis ♂

188 Kirbya pacifica ♂

189 Cleonice
♂ bigelowi ♀

190 Chaetonopsis spinosa ♂

Figs. 110.179–190. Dorsal views of scutellum: (179) *Cyzenis albicans* (Fallén); (180) *Cyzenis mitis* (Curran); (181) *Graphogaster dorsalis* (Coquillett); (182) *Actia interrupta* Curran; (183) *Neomintho celeris* (Townsend); (184) *Eucelatoria armigera* (Coquillett); (185) *Eucelatoria leucophaeata* (Reinhard); (186) *Phyllophilopsis nitens* (Coquillett); (187) *Voria ruralis* (Fallén); (188) *Kirbya pacifica* (Curran); (189) *Cleonice bigelowi* (Curran); (190) *Chaetonopsis spinosa* (Coquillett). Abbreviations: ap, apical; b, basal; ds, discal; l, lateral; preap s, preapical bristle; sbap, subapical; sctl s, scutellar bristle.

Mid tibia with well-developed anterodorsal bristle (as in Fig. 221). Lower katepimeral bristle usually larger than anterodorsal katepimeral bristle. First aristomere minute, no longer than wide; third aristomere much more than twice as long as first and second combined .... ***Ceranthia*** Robineau-Desvoidy[42]
6 spp.; widespread; Curran 1933, in part (as *Actia*)

170. R$_{4+5}$ setose from base to well beyond crossvein r-m (Fig. 200) 171
R$_{4+5}$ not setose beyond crossvein r-m (as in Fig. 199) 172

171. Katepisternum with a row of fine hairs ascending from midventral angle of katepisternum to a point just ventral to lower katepisternal bristle. Upper part of anepisternum usually with two well-developed bristles. Parafacial usually without minute setae below lowest frontal bristle .... ***Actia*** Robineau-Desvoidy
5 spp.; widespread; Curran 1933, in part

Katepisternum lacking such a row of fine hairs. Upper part of anepisternum usually with a single well-developed bristle. Parafacial with minute setae extending from lowest frontal bristle usually to level of base of arista .... ***Ceromya*** Robineau-Desvoidy[43]
4 spp.; widespread; Curran 1933, in part (as *Actia*)

172. Scutellum lacking both lateral and discal bristles (as in Fig. 186). Membrane between lower genal margin and clypeus forming a convex sclerite (Figs. 144, 152) .... ***Ginglymia*** Townsend[44]
2 spp.; western and eastern

Scutellum with small lateral bristles and well-developed discal bristles (as in Fig. 184). No sclerite between genal margin and clypeus 173

173. Facial ridge bare, except for a few setae just above vibrissa. Middle katepisternal bristle almost in line with anterior and posterior katepisternal bristles ...... ***Phantasiomyia*** Townsend
2 spp.; western

Facial ridge with bristles on lower half or more. Middle katepisternal bristle ventral to other two 174

174. R$_1$ setose dorsally (as in Fig. 200) .... ***Miamimyia*** Townsend
1 sp., *cincta* Townsend; southern Florida

R$_1$ bare .... ***Chaetonodexodes*** Townsend, in part
see couplet 142

175. Hind coxa with one or more hairs on posterior margin (Fig. 229) 176
Hind coxa bare on posterior margin (as in Fig. 230) 191

176. Parafacial with one or two bristles; these distinctly larger than surrounding hairs and situated near lower margin of eye (Figs. 62, 63) 177
Parafacial with hairs only or bare 179

177. Palpus present, filiform, not enlarged apically (Fig. 62)...... ***Peleteria*** Robineau-Desvoidy
39 spp.; widespread; Curran 1925

Palpus absent 178

178. Parafacial with two stout bristles; these more or less equal in size, separated from each other by about half distance between upper parafacial bristle and lowest frontal bristle (as in Fig. 62). Frontal bristles arising in two rows, the lowest bristle at level of lower fourth of eye .... ***Deopalpus*** Townsend
11 spp.; widespread; Reinhard 1934*c* (as *Cuphocera*)

Parafacial usually with a single stout bristle, sometimes with a smaller bristle immediately below it (Fig. 63). Frontal bristles arising in a single row, lowest bristle at level of middle of eye .... ***Copecrypta*** Townsend
1 sp., *ruficauda* (Wulp); widespread

179. Palpus well-developed 180
Palpus absent or reduced to a minute tubercle 188

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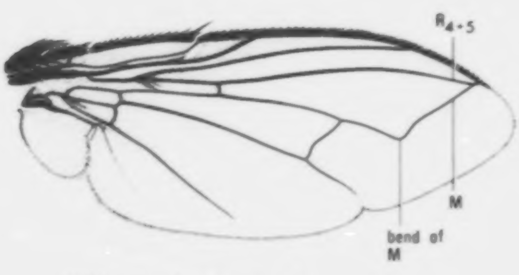
[42] This is a provisional placement for several species, *viz. arizonica* (Townsend), *brevirostris* (Coquillett), *conata* (Reinhard), *flavipes* (Coquillett), and *plusiae* (Coquillett), formerly included in *Aphantorhapha* Townsend, *Pseudosiphona* Townsend, and *Siphona* Meigen.

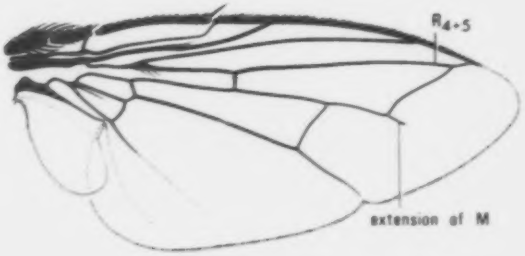
[43] Included here are four species, *americana* (Townsend), *elyii* (Walton), *ontario* (Curran), and *palloris* (Coquillett), formerly included in *Actia*.

[44] Also included are species formerly in the genus *Lasioneura* Coquillett.



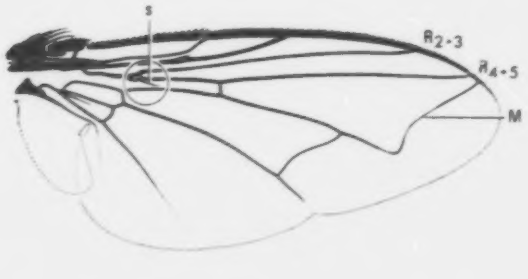
R_{4+5}
M
bend of M

191 Tryphera sp. ♂

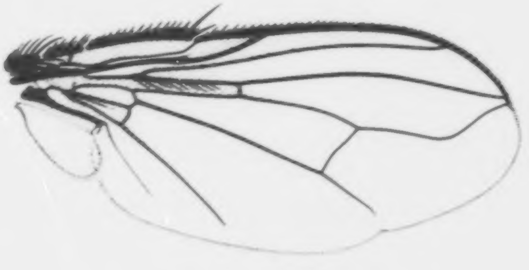


R_{4+5}
extension of M

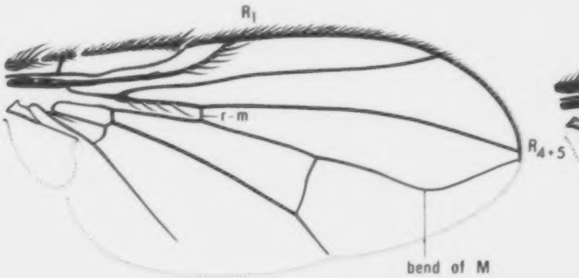
192 Hesperomyia erythrocera ♂



193 Drino antennalis ♂

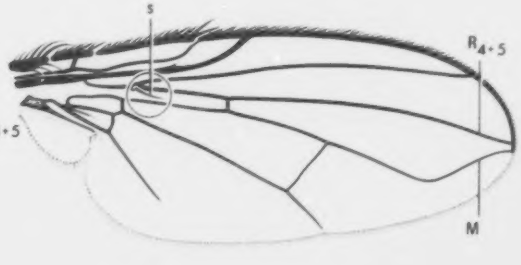


194 Masistylum stennomatum ♂

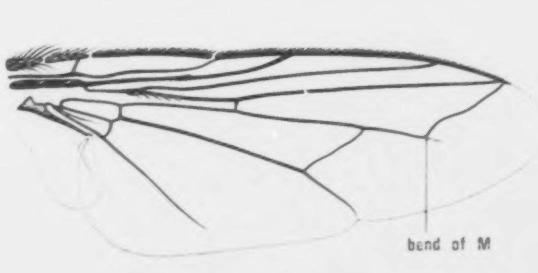


R_1
r-m
R_{4+5}
bend of M

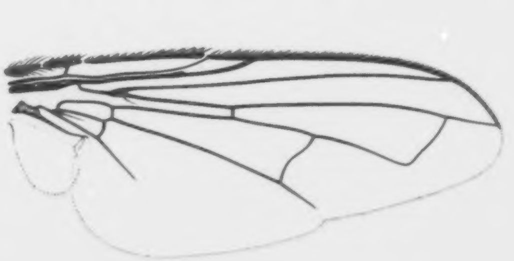
195 Chaetostigmoptera crassinervis ♂



196 Phytomyptera tarsalis ♂



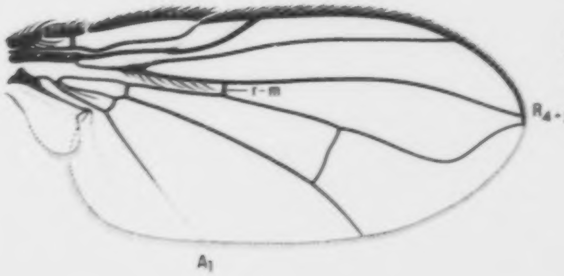
197 Chetogena gelida ♂



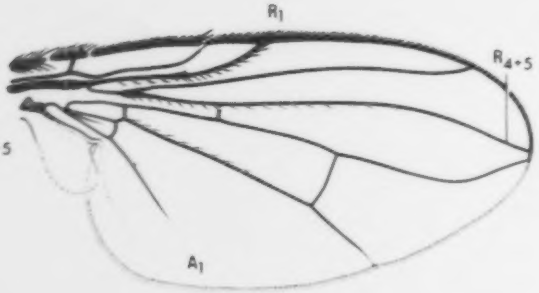
198 Graphogaster brunnea ♂

Figs. 110.191–198. Dorsal views of right wing: (191) *Tryphera* sp.; (192) *Hesperomyia erythrocera* Brauer & Bergenstamm; (193) *Drino antennalis* (Reinhard); (194) *Masistylum stennomatum* Wood; (195) *Chaetostigmoptera crassinervis* (Walton); (196) *Phytomyptera tarsalis* (Coquillett); (197) *Chetogena gelida* (Coquillett); (198) *Graphogaster brunnea* (Brooks) (*continued*).

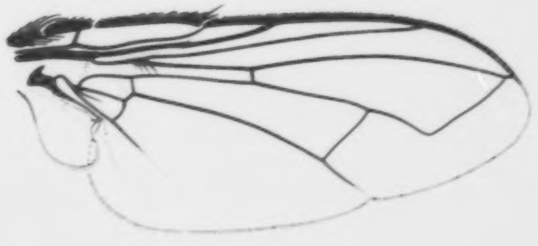
Abbreviation: s, seta at bifurcation of R_{2+3} and R_{4+5}.



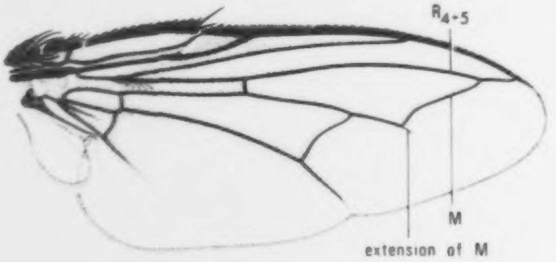
199 Ceranthia flavipes ♀



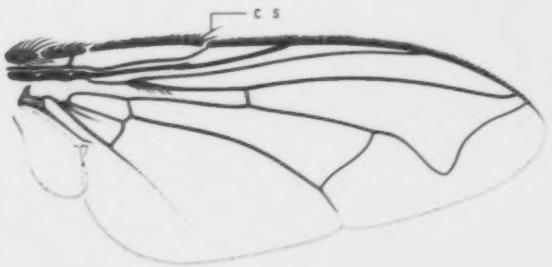
200 Actia interrupta ♀



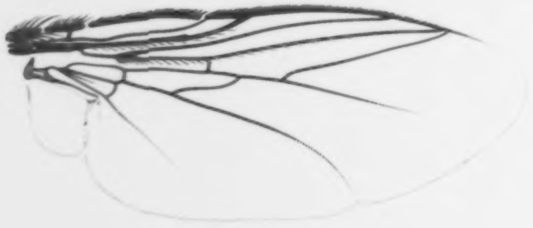
201 Estheria cinerea ♂



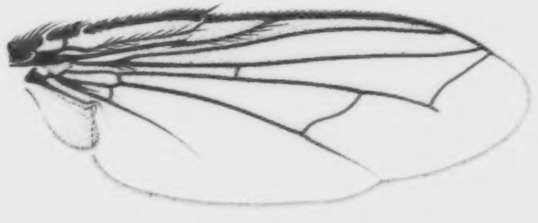
202 Microchaetina sinuata ♂



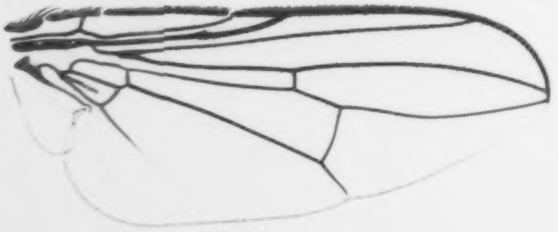
203 Megapariopsis opaca ♂



204 Goniochaeta plagioides ♀

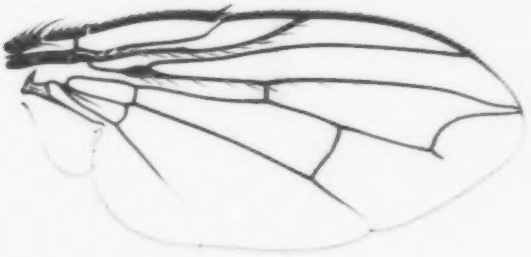


205 Chaetoplagia atripennis ♂

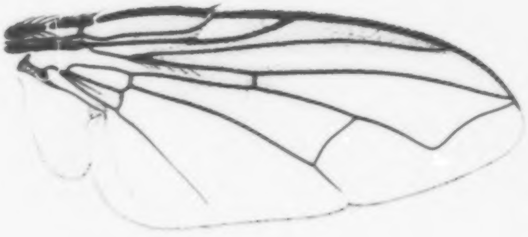


206 Freraea montana ♂

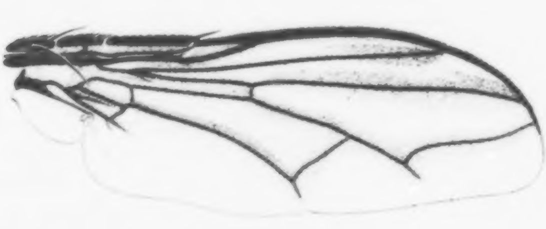
Figs. 110.199–206. Wings: dorsal views of right wing (*continued*) of (199) *Ceranthia flavipes* (Coquillett), (200) *Actia interrupta* Curran, (201) *Estheria cinerea* (Townsend), (202) *Microchaetina sinuata* (Townsend), (203) *Megapariopsis opaca* (Coquillett), and (204) *Goniochaeta plagioides* Townsend; ventral view of left wing of (205) *Chaetoplagia atripennis* Coquillett; dorsal view of right wing of (206) *Freraea montana* (Coquillett) (*continued*).



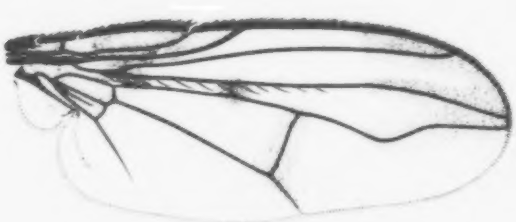
207 Lypha harringtoni ♂



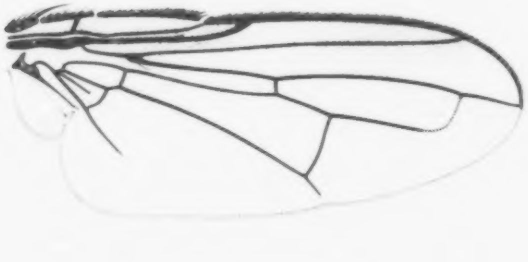
208 Myothyriopsis picta ♂



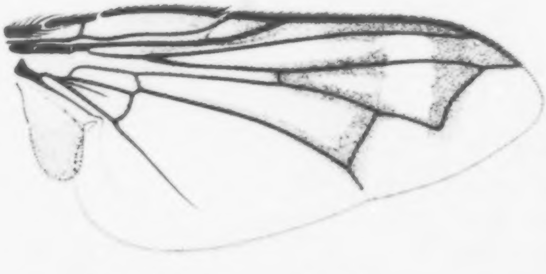
209 Euantha litturata ♂



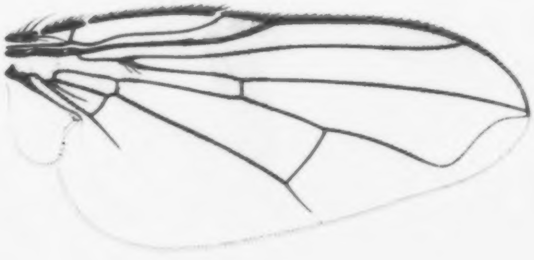
210 Chiricahuia sp. ♀



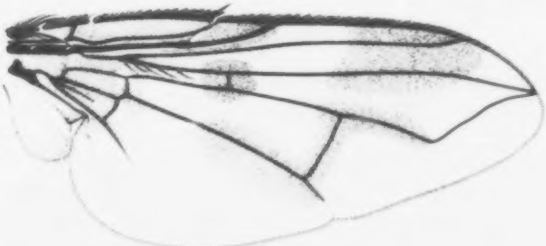
211 Catharosia lustrans ♂



212 Euthera tentatrix ♂

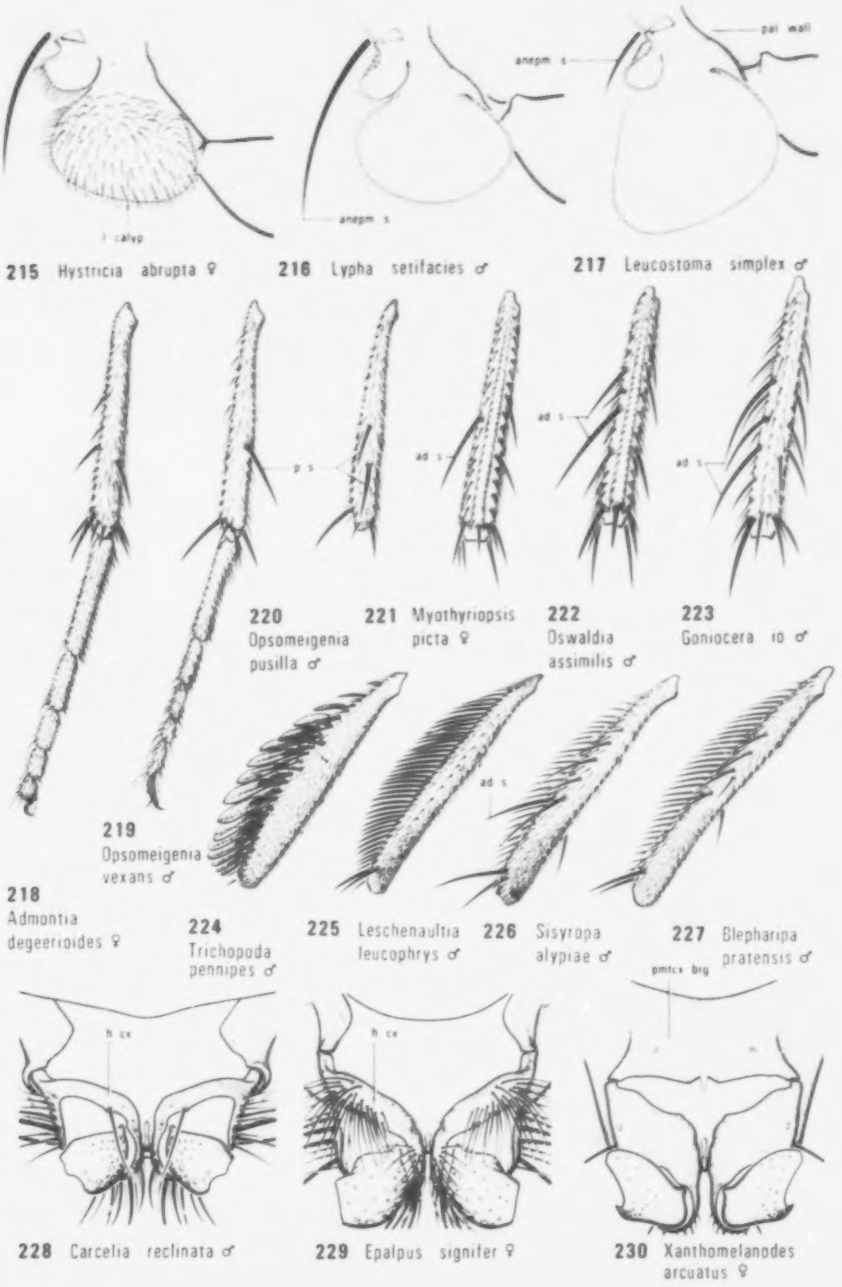


213 Oestrophasia signifera ♂



214 Oestrophasia clausa ♀

Figs. 110.207–214. Dorsal views of right wing (*concluded*): (207) *Lypha harringtoni* (Coquillett); (208) *Myothyriopsis picta* (Wulp); (209) *Euantha litturata* (Olivier); (210) *Chiricahuia* sp.; (211) *Catharosia lustrans* (Reinhard); (212) *Euthera tentatrix* Loew; (213) *Oestrophasia signifera* (Wulp); *Oestrophasia clausa* Brauer & Bergenstamm.



215 Hystricia abrupta ♀ **216** Lypha setifacies ♂ **217** Leucostoma simplex ♂

218 Admontia degeerioides ♀ **219** Opsomeigenia vexans ♂ **220** Opsomeigenia pusilla ♂ **221** Myothyriopsis picta ♀ **222** Oswaldia assimilis ♂ **223** Goniocera io ♂

224 Trichopoda pennipes ♂ **225** Leschenaultia leucophrys ♂ **226** Sisyropa alypiae ♂ **227** Blepharipa pratensis ♂

228 Carcelia reclinata ♂ **229** Epalpus signifer ♀ **230** Xanthomelanodes arcuatus ♀

Figs. 110.215–230. Calypteres, legs, and hind coxae: dorsal views of left calypter of (215) *Hystricia abrupta* (Wiedemann), (216) *Lypha setifacies* (West), and (217) *Leucostoma simplex* (Fallén); lateral views of left foreleg of (218) *Admontia degeerioides* (Coquillett) and (219) *Opsomeigenia vexans* (Curran); (220) dorsal view of left fore tibia of *Opsomeigenia pusilla* (Coquillett); dorsal views of mid tibia of (221) *Myothyriopsis picta* (Wulp), (222) *Oswaldia assimilis* (Townsend), and (223) *Goniocera io* (Aldrich); posterior views of hind tibia of (224) *Trichopoda pennipes* (Fabricius), (225) *Leschenaultia leucophrys* (Wiedemann), (226) *Sisyropa alypiae* Sellers, and (227) *Blepharipa pratensis* (Meigen); posteroventral views of hind coxa and postmetacoxal area of (228) *Carcelia reclinata* (Aldrich & Webber), (229) *Epalpus signifer* (Walker), and (230) *Xanthomelanodes arcuatus* (Say).

Abbreviations: ad s, anterodorsal bristle; anepm s, anepimeral bristle; h cx, hind coxa; l calyp, lower calypter; pal wall, postalar wall; pmtcx brg, postmetacoxal bridge; p s, posterior bristle.

180. Eye covered with conspicuous dense hairs 181

Eye apparently bare 182

181. Abdominal tergites 3 and 4 each with only one pair of median discal bristles .... ***Jurinia*** Robineau-Desvoidy

2 spp.: eastern

Abdominal tergites 3 and 4 almost completely covered with discal bristles (as in Fig. 234) .... ***Jurinella*** Brauer & Bergenstamm

1 sp., *lutzi* Curran: southwestern: Curran 1947

182. Palpus longer than height of head, flattened and parallel-sided, extending forward far beyond lower facial margin (Fig. 145); proboscis long and slender, 1.5 or more times height of head .... ***Adejeania*** Townsend

1 sp., *vexatrix* (Osten Sacken): western: Curran 1947

Palpus not as long as head height, usually distinctly clubbed apically, but if apparently parallel-sided (as in *Protodejeania*), then narrower than proboscis 183

183. Abdominal tergite 3 with only one pair of median marginal bristles 184

Abdominal tergite 3 with more than one pair (usually three or more pairs) of median marginal bristles (Fig. 241) 185

184. First flagellomere, even in male, small, subcircular, bluntly rounded or truncate apically, always shorter than pedicel (Fig. 129) .... ***Tachina*** Meigen[45]

39 spp.: widespread: Tothill 1924, Rowe 1931 (as *Fabriciella*)

First flagellomere kidney-shaped, somewhat pointed apically, in most species as long as, or longer than, pedicel, even in female (Fig. 130); if first flagellomere shorter than pedicel (some females), then abdominal tergites 2–4 bluish pruinose, contrasting with nonpruinose tergite 5 .... ***Archytas*** Jaennicke

13 spp.: widespread: Ravlin and Stehr 1984

185. Abdominal tergites 3 and 4 each with a complete transverse row of marginal bristles displaced anteriorly at midline enclosing a small patch of bristles between it and posterior margin of tergite (Fig. 240) .... ***Paradejeania*** Brauer & Bergenstamm

1 sp., *rutilioides* (Jaennicke): southwestern: Arnaud 1951

Marginal bristles all more or less equidistant from posterior margin of tergite (Fig. 241) 186

186. Abdominal tergites 3 and 4 without median discal bristles; tergite 3 with three to five pairs of short stout median marginal bristles; the longest of these no more than twice as long as the shortest (Fig. 241) .... ***Juriniopsis*** Townsend

4 spp.: southern: Sabrosky 1969

Abdominal tergites 3 and 4 each with several pairs of discal bristles forming a median patch or irregular transverse row; tergite 3 with a single pair of median marginal bristles and several much shorter ones less than a third their length (as in Fig. 242) 187

187. Base of wing and a small area around crossvein r-m darkened. Abdomen dark brown .... ***Pararchytas*** Brauer & Bergenstamm

2 spp.: widespread

Base of wing and area surrounding crossvein r-m not noticeably darker. Abdomen orange or reddish .... ***Protodejeania*** Townsend

2 spp.: western: Curran 1947

188. Abdomen black except for a triangular spot of white or gold pollen on tergite 5; tergite 3 with two or three pairs of median marginal bristles; tergite 4 with group of discal bristles (Fig. 242) .... ***Epalpus*** Rondani

3 spp.: widespread

Abdomen orange, brown, or yellow with black apex; tergite 3 with more than four pairs of median marginal bristles; tergite 4 without discal bristles (Fig. 243) 189

189. Abdomen pale yellow on basal half, black on all of tergite 5 and adjacent margin of tergite 4 .... ***Xanthoepalpus*** Townsend

1 sp., *bicolor* (Williston): western

Abdomen predominently unicolorous, orange or brown 190

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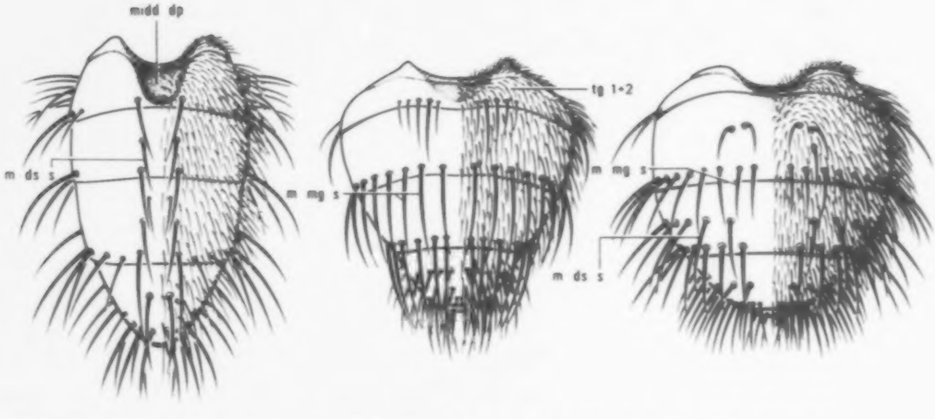
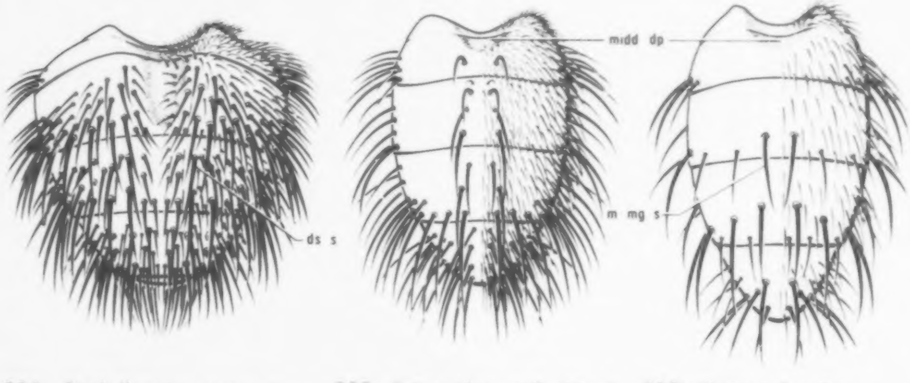
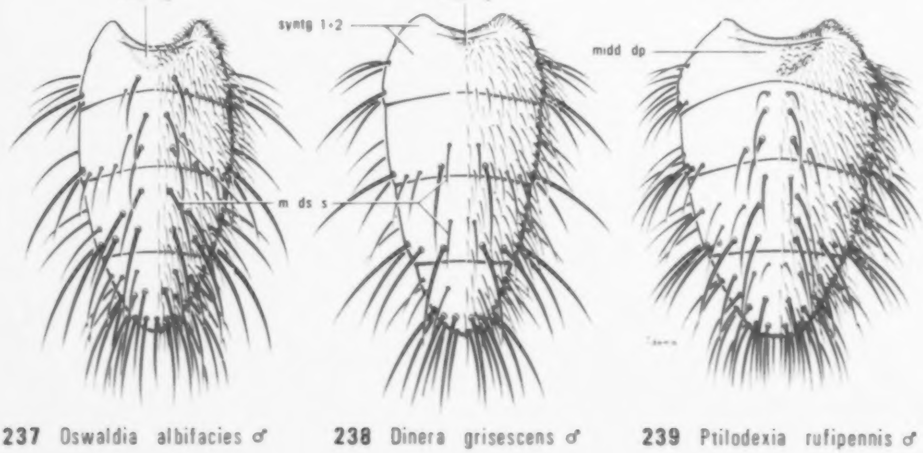
[45] Included here are all species formerly placed in *Metopotachina* Townsend and *Nowickia* Wachtl.



231 Blondelia hyphantriae ♂ **232** Diotrephes atriventris ♂ **233** Chlorohystricia cyaneiventris ♂



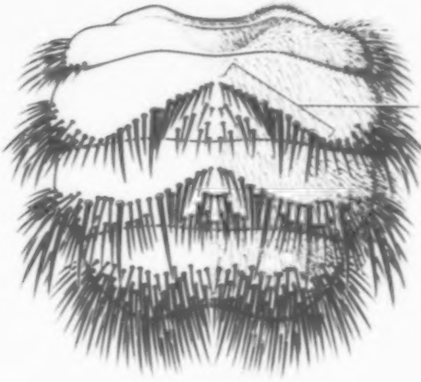
234 Bombyliomyia soror ♂ **235** Pelatachina pellucida ♂ **236** Chaetonodexodes vanderwulpi ♂



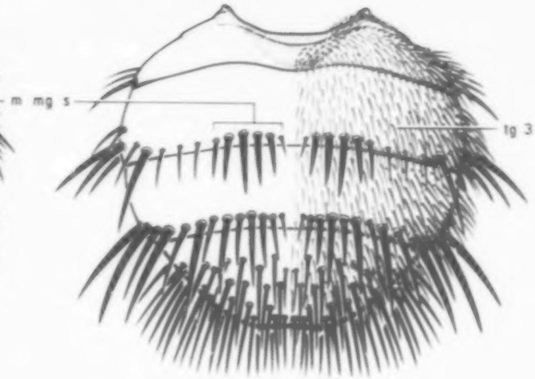
237 Oswaldia albifacies ♂ **238** Dinera grisescens ♂ **239** Ptilodexia rufipennis ♂

Figs. 110.231-239. Dorsal views of abdomen: (231) *Blondelia hyphantriae* (Tothill); (232) *Diotrephes atriventris* (Walker); (233) *Chlorohystricia cyaneiventris* (Wulp); (234) *Bombyliomyia soror* (Williston); (235) *Pelatachina pellucida* Coquillett; (236) *Chaetonodexodes vanderwulpi* (Townsend); (237) *Oswaldia albifacies* (Townsend); (238) *Dinera grisescens* (Fallén); (239) *Ptilodexia rufipennis* (Macquart) (*continued*).

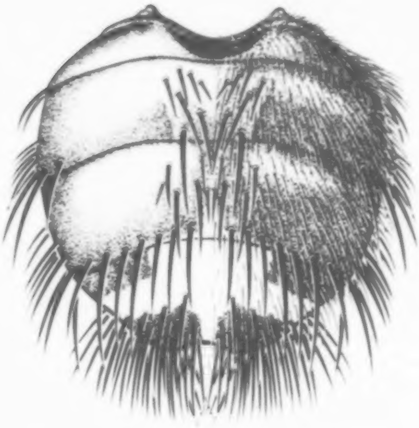
Abbreviations: ds s, discal bristle; m ds s, median discal bristle; midd dp, middorsal depression; m mg s, median marginal bristle; syntg, syntergite; tg, tergite.



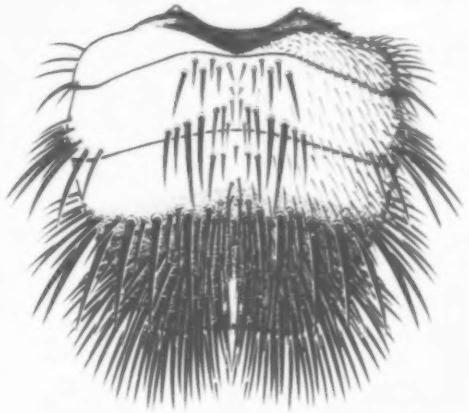
240 Paradejeania rutilioides ♀



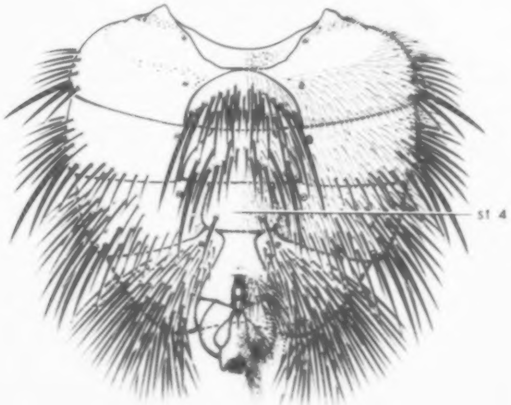
241 Juriniopsis floridensis ♀



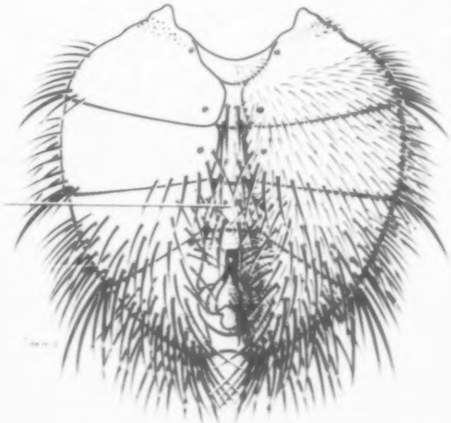
242 Epalpus signifer ♀



243 Xanthoepalpus bicolor ♀



244 Rhachoepalpus olivaceus ♂



245 Parepalpus flavidus ♂

Figs. 110.240–245. Abdomens: dorsal views of abdomen (*concluded*) of (240) *Paradejeania rutilioides* (Jaennicke), (241) *Juriniopsis floridensis* Townsend, (242) *Epalpus signifer* (Walker), and (243) *Xanthoepalpus bicolor* (Williston); ventral views of abdomen of male of (244) *Rhachoepalpus olivaceus* Townsend and (245) *Parepalpus flavidus* Coquillett. Abbreviations: m mg s, median marginal bristle; st, sternite; tg, tergite.

190. Abdomen orange; abdominal sternites narrow, overlapped by ventral edges of tergites (Fig. 245); tergite 3 with a pair of median marginal bristles and a single pair of median discal bristles .... ***Parepalpus*** Coquillett

1 sp., *flavidus* Coquillett; western; Curran 1947

Abdomen ochrous brown pruinescent, shinier and somewhat darker laterally and on apex of tergite 5; abdominal sternites broad, heavily bristled, overlapping tergites (Fig. 244); tergite 3 with uninterrupted row of marginal bristles .... ***Rhachoepalpus*** Townsend

1 sp., *olivaceus* Townsend; Arizona; Curran 1947

191. All four of the following characters present simultaneously (Fig. 64): only one frontal bristle arising below upper margin of pedicel; pedicel with one or two exceptionally long slender setae which are more than half as long as arista; arista pubescent or plumose; subvibrissal ridge with five or more slender bristles usually continuous with bristles of subcranial margin. Male with upper frontal bristles proclinate (Figs. 54, 55, 64) 192

Differing from the above in the following: frontal bristles usually descending below level of pedicel (Figs. 63, 65), but if not, then either setae on pedicel all shorter than half aristal length or arista minutely pubescent or apparently bare; subvibrissal ridge usually with fewer than five bristles, usually not continuous with bristles along subvibrissal ridge. Male with upper frontal bristles reclinate 218

192. Proepisternum setose (as in Fig. 166) 193

Proepisternum bare (as in Fig. 167), rarely with a single hair 204

193. Proboscis long, slender, anteriorly curved at apex, more than twice as long as head height (Fig. 147) .... ***Prosenoides*** Brauer & Bergenstamm

3 spp.; western and southern; Reinhard 1954

Proboscis at most 1.5 times as long as head height 194

194. M ending in R_{4+5} before reaching wing margin (as in Fig. 191) .... ***Estheria*** Robineau-Desvoidy, in part

1 sp., *cinerea* (Townsend); western

M ending separately in wing margin 195

195. Middorsal depression on abdominal syntergite 1 + 2 confined to anterior half or less of that segment (Fig. 238). Median marginal bristles on this syntergite normally absent....... .... ***Dinera*** Robineau-Desvoidy

1 sp., *grisescens* (Fallén); widespread

Middorsal depression on abdominal syntergite 1 + 2 extending back to hind margin of that segment, or if not, then one pair of erect median marginal bristles present 196

196. Large heavily spined species, over 1 cm long. Katepisternum with four or more bristles. Abdominal tergite 3 with transverse row of three or more pairs of median marginal bristles. Female abdomen entirely dark brown; abdomen of male brown on tergites 1-3, gold pruinescent on tergites 4 and 5 .... ***Euchaetogyne*** Townsend

1 sp., *roederi* (Williston); Arizona, New Mexico

Smaller more slender species than above, with fewer katepisternal and marginal bristles. Abdominal features not as above 197

197. Integument and pruinescence entirely pale orange brown. Proboscis and palpus both exceptionally short, shorter than arista. Lower half of face, in anterior view, high and narrow; vibrissa arising above lower facial margin (Fig. 80) .... ***Phasiops*** Coquillett

1 sp., *flavus* Coquillett; eastern U.S.A.

Integument dark brown or black, with grayish pruinescence. Proboscis well-developed. Palpus either normally developed or absent. Lower half of face not narrowed, and vibrissa arising at level of lower facial margin (Figs. 83, 84) 198

198. Middorsal depression on abdominal syntergite 1 + 2 confined to anterior two-thirds of that segment (as in Fig. 237) .... ***Phalacrophyto*** Townsend

1 sp., *sarcophagina* (Coquillett); southcentral U.S.A.

Middorsal depression on abdominal syntergite 1 + 2 reaching to or nearly to hind margin of that segment (as in Fig. 239) 199

199. Face with at most a small carina that scarcely separates antennae (Fig. 83) .... ***Billaea*** Robineau-Desvoidy[46]

9 spp.; widespread

Face with a prominent median carina, usually high enough to separate the antennae along their entire length (Fig. 84) 200

200. Parafacial with setae over most of its length (as in Figs. 77–79) .... ***Dolichocodia*** Townsend

2 spp.; southwestern

Parafacial bare or with a few minute scattered setae 201

201. Proboscis slender, straight, about as long as height of head. Hind tibia of male with comb-like dorsolateral row of short evenly and closely set setae (as in Fig. 227) .... ***Opsotheresia*** Townsend

2 spp.; eastern

Proboscis stouter, shorter than height of head. Hind tibia of male without comb-like row of setae 202

202. Facial carina widest and most prominent ventrally, below level of apices of antennae .... ***Dexia*** Meigen

1 introduced sp., *ventralis* Aldrich; New Jersey

Facial carina widest and most prominent near middle of face, between antennae 203

203. Facial carina of rather uniform height, flattened along its crest, in anterior view widest near its midpoint, just below level of base of arista. Inner vertical bristles parallel or divergent (Fig. 54). Anterior genal margin straight or slightly concave, ending ventrally below eye well behind its midpoint .... ***Nicephorus*** Reinhard

1 sp., *floridensis* Reinhard; southeastern

Facial carina more conical, most prominent at level of junction of pedicel and first flagellomere, with rounded crest (Fig. 84). Apices of inner vertical bristles convergent. Anterior genal margin convex, sometimes with a few small hairs extending across membrane of genal groove to lower corner of face .... ***Arctophyto*** Townsend[47]

14 spp.; widespread; Curran 1924

204. Middorsal depression of abdominal syntergite 1 + 2 extending back to hind margin of that segment (as in Fig. 239) 205

Middorsal depression of syntergite 1 + 2 smaller and shallower, not extending back to hind margin (as in Fig. 238) 212

205. M ending in R_{4+5} before reaching wing margin (as in Fig. 191) 206

M ending separately in wing margin (as in Fig. 193) 208

206. Proboscis exceptionally long and slender, longer than height of head, and curving forward apically (as in Fig. 110) .... ***Nimioglossa*** Reinhard

2 spp.; southwestern

Proboscis shorter than head height 207

207. Parafacial with short stout setae. Bend of M acute, the part beyond bend sinuous (as in Fig. 203). Proboscis exceptionally short. Face strongly narrowed in frontal view .... ***Megaparia*** Wulp

1 sp., *venosa* Wulp; southwestern

Parafacial bare. Bend of M obtuse, the part beyond bend nearly straight. Proboscis and face not so modified .... ***Orestilla*** Reinhard

1 sp., *primoris* Reinhard; southwestern

208. Proboscis long and slender, longer than height of head (as in Fig. 110) 209

Proboscis shorter and stouter, not as long as head height 210

209. Face with a broad, flat-topped carina, completely separating antennae (as in Fig. 84) .... ***Prosena*** Lepeletier & Serville

1 introduced sp., *siberita* (Fabricius); eastern U.S.A.

Face without a median carina .... ***Mochlosoma*** Brauer & Bergenstamm

5 spp.; widespread; Reinhard 1958*b*

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[46] Included here are all species formerly placed in *Eutheresia* Townsend, *Paratheresia* Townsend, and *Theresia* Robineau-Desvoidy.

[47] Also included here are the species formerly placed in *Ateloglossa* Coquillett, *Carinosillus* Reinhard, and *Vibrissotheresia* Reinhard.

210. Fronto-orbital plate outside of row of frontal bristles almost devoid of setae except near ocellar triangle (Fig. 55). Abdomen strongly pointed apically, especially in male .... ***Zelia*** Robineau-Desvoidy[48]

12 spp.; widespread

Fronto-orbital plate with setae outside frontal bristles extending forward to below middle of eye. Abdomen rounded apically 211

211. Abdominal tergites 3 and 4 each with weak, recumbent marginal bristles, but without discal bristles. An exceptionally large species, usually longer than 30 mm, with broad, uniformly dark brown abdomen .... ***Trixodes*** Coquillett

1 sp., *obesus* Coquillett; southwestern

Abdominal tergites 3 and 4 each with strong erect marginal and discal bristles, the latter usually present as two pairs with one situated before the other (Fig. 239). Moderate-sized, about 10–15 mm long. Abdomen narrower, tapering, usually with variegated pruinose pattern .... ***Ptilodexia*** Brauer & Bergenstamm

23 spp.; widespread; Wilder 1979

212. M ending in R_{4+5} before reaching wing margin (as in Figs. 192, 198) 213

M ending separately in wing margin (as in Fig. 193) 214

213. Fused portion of R_{4+5} and M shorter than crossvein r-m (Fig. 201); second costal portion (between apices of Sc and R_1) three or more times as long as costal bristle (as in Fig. 203) .... ***Estheria*** Robineau-Desvoidy, in part

see couplet 194

Fused portion of R_{4+5} and M longer than crossvein r-m; second costal portion less than twice as long as costal bristle (Fig. 202) .... ***Microchaetina*** Wulp, in part

see couplet 101; Reinhard 1942*a* (in part, as *Hypenomyia*)

214. Proboscis and palpus both exceptionally short, shorter than arista. Lower part of face, at and below level of vibrissae, narrowed, not protruding (as in Fig. 150). First flagellomere no longer than pedicel 215

Proboscis and palpus not so modified. Lower part of face not strongly narrowed (as in Fig. 149). First flagellomere distinctly longer than pedicel 216

215. Parafacial with short stout setae. Bend of M acute, exceptionally close to hind margin of wing; the part beyond bend sinuous (Fig. 203). Clypeus long and narrow (Fig. 150). .... ***Megapariopsis*** Townsend

1 sp., *opaca* (Coquillett); southeastern U.S.A.

Parafacial bare. Bend of M obtuse. Clypeus inverted U-shaped (Fig. 151) .... ***Eumegaparia*** Townsend

1 sp., *flaveola* (Coquillett); western

216. Abdominal syntergite 1 + 2 elongate and strongly constricted to form a cylindrical petiole .... ***Cordyligaster*** Macquart

1 sp., *septentrionalis* Townsend; eastern U.S.A.

Base of abdomen not petiolate 217

217. Wing strongly patterned, with the veins emphasized with dark brown (Fig. 209). Body predominantly yellow. Abdominal syntergite 1 + 2 without marginal bristles .... ***Euantha*** Wulp

1 sp., *litturata* (Olivier); central and eastern U.S.A.

Wing unpatterned. Body blue gray. Abdominal syntergite 1 + 2 with one pair of median marginal bristles .... ***Ochrocera*** Townsend

1 sp., *vaginalis* Townsend; northeastern U.S.A., Quebec, Ontario

218. Scutellum with one to three straight nearly erect preapical bristles arising on dorsal surface just anterior to apex (Figs. 187, 188). Anterior margin of postgena with at most a slight genal dilation (Figs. 65–76). Last section of CuA_1 (beyond crossvein dm-cu) between half as long (Fig. 205) and twice as long (Fig. 204) as preceding section 219

Scutellum without a group of one to three long straight preapical bristles. Anterior margin of postgena usually with well-developed genal dilation. Last section of CuA_1 usually less than half as long as preceding section (as in Figs. 207–214) 235

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[48] Also included here are all species of the genera *Metadexia* Coquillett and *Minthozelia* Townsend.

219. Anepimeron with an exceptionally long stout bristle, extending beyond apex of lower calypter (as in Figs. 215, 216) 220

Anepimeron with at most a short bristle not extending beyond middle of lower calypter (as in Fig. 217) 222

220. Ultimate section of CuA_1 twice as long as preceding section (Fig. 204); extension of M beyond bend longer than portion of M between crossvein r-m and bend .... ***Goniochaeta*** Townsend, in part

2 spp.; western

Ultimate section of CuA_1 about equal to or shorter than preceding section 221

221. Parafacial with two or three long proclinate bristles (Fig. 65). R_1 and CuA_1 without setae dorsally .... ***Athrycia*** Robineau-Desvoidy

1 sp., *cinerea* (Coquillett); widespread

Parafacial with only a few short setae below lowest frontal bristle (Fig. 66). R_1, R_{4+5}, and CuA_1 setose dorsally (as in Fig. 200) .... ***Hypovoria*** Villeneuve[49]

2 spp.; widespread

222. M ending in R_{4+5} well before wing margin (as in Figs. 198, 202, 212) 223

M ending separately in wing margin (as in Figs. 193, 205, 209) 225

223. Parafacial bristles arising in a row along anterior margin of parafacial, flanked laterally by smaller setae; none arising from a shiny black spot (Fig. 67) .... ***Uclesia*** Girschner

3 spp.; western; Curran 1927*a*

Parafacial bristles arising nearer middle of parafacial; one or more usually arising from a shiny black spot (Figs. 68–70) 224

224. Abdominal tergite 4, and usually 3 also, with median marginal bristles .... ***Wagneria*** Robineau-Desvoidy

5 spp.; widespread; Reinhard 1955, in part

Abdominal tergites 3 and 4 each lacking differentiated marginal and discal bristles .... ***Kirbya*** Robineau-Desvoidy[50]

5 spp.; widespread; Curran 1927*a* (as *Hesperophasia*)

225. Parafacial with a single large proclinate bristle arising just below lowest frontal bristle (Fig. 71) .... ***Voria*** Robineau-Desvoidy

1 species complex; widespread

Parafacial with a row of proclinate bristles or patch of small decumbent setae (Figs. 72–76) 226

226. Eye covered with long dense hairs (Fig. 72) .... ***Cyrtophleba*** Rondani[51]

3 spp.; widespread

Eye apparently bare (as in Figs. 73–76) 227

227. Sc with bristles ventrally; R_1 usually setose ventrally as well as dorsally, at least at apex (Fig. 205) .... ***Chaetoplagia*** Coquillett

1 sp., *atripennis* Coquillett; widespread

Sc and R_1 bare ventrally 228

228. Parafacial setae small and short, more or less uniform in length, none distinctly bristle-like (as in Fig. 66) 229

Parafacial setae composed of bristles and hairs, differing distinctly in size, the bristles usually arranged in a vertical row (Figs. 73–76) 230

229. Prementum slender, straight and as long as or longer than height of head; labella reduced, pointed apically (Fig. 148) .... ***Plagiomima*** Brauer & Bergenstamm

10 spp.; widespread in U.S.A.; Aldrich 1926*a*

Prementum shorter than head height; labella usually enlarged .... ***Metaplagia*** Coquillett[52]

6 spp.; widespread

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[49] Included here are the two species formerly placed in *Catalinovoria* Townsend.

[50] This genus includes all species formerly placed in the tribe Hesperophasiini, *viz.* *Coleophasia* Townsend, *Hesperophasia* Townsend, and *Hesperophasiopsis* Townsend. The genus belongs to the tribe Voriini.

[51] Also included here is *Eucyrtophloeba* Townsend.

[52] Also included here are the species formerly placed in *Anzamyia* Reinhard and *Metavoria* Townsend.

230. Parafacial bristles confined to lower part of parafacial; some of the largest arising on membrane between parafacial and ptilinal suture and on adjacent genal groove, anterior to silvery pruinose area of parafacial (Fig. 73) . . . . **Menetus** Aldrich

1 sp., *macropogon* (Bigot), California

Parafacial bristles all arising from silvery pruinose area of parafacial 231

231. Vibrissal axis (length of subcranial cavity) greater than antennal axis (distance from antennal base to back of head). Lower facial margin strongly protruding (Fig. 74). Lateral margins of subcranial cavity pinched in below eye . . . . **Chaetovoria** Villeneuve

1 sp., *seriata* (Aldrich); western, alpine

Vibrissal axis less than antennal axis. Lower facial margin scarcely protruding (Fig. 76) or not visible in profile (Fig. 75). Lateral margins of subcranial cavity straight or convex 232

232. Second aristomere elongate, more than 3 times as long as wide (Fig. 131) 233

Second aristomere not more than twice as long as wide 234

233. Parafacial bristles arising close to ptilinal suture on a slightly raised ridge, which in profile obscures suture and that part of parafacial between suture and row of bristles. Lower facial margin not visible in profile . . . . **Psilopleura** Reinhard

1 sp., *arida* Reinhard; southwestern

Parafacial bristles more removed from ptilinal suture; portion of parafacial between bristles and suture distinctly visible in profile (Fig. 76) . . . . **Euptilopareia** Townsend

2 spp.; widespread

234. Genal area greatly enlarged; subvibrissal ridge and subcranial margin together with about 10 or more bristles (Fig. 75). Arista thickened nearly to apex . . . . **Cockerelliana** Townsend

1 sp., *capitata* Townsend; southwestern

Genal area much smaller; subvibrissal ridge and subcranial margin with about five bristles (as in Fig. 76). Arista thickened on at most basal two-thirds . . . . **Meleterus** Aldrich

2 spp.; eastern and southwestern

235. Parafacial setose on lower half or more (as in Figs. 89–97) 236

Parafacial bare at least on lower half 271

236. M ending in R_{4+5} well before wing margin; the united petiole at least half as long as that part of M beyond bend (Figs. 198, 211) 237

M ending separately in wing margin or in R_{4+5} very close to margin (Fig. 195) 251

237. Arista pubescent (as in Fig. 125) 238

Arista bare 239

238. M joining R_{4+5} nearly at right angles; wing mostly or entirely darkly pigmented (Fig. 4.75) . . . . **Melanophora** Meigen (see Rhinophoridae, Ch. 109)

M joining R_{4+5} at an acute angle; wing transparent . . . . **Orthosimyia** Reinhard

2 spp.; California

239. Abdominal tergites 3 and 4 lacking differentiated marginal and discal bristles. Small shining black species with fronto-orbital plate and all of parafacial shining black contrasting with thickened orange brown arista and antennal base (Fig. 77) . . . . . . **Euscopolia** Townsend

1 sp., *dakotensis* Townsend; widespread

Abdominal tergite 4, and usually 3 also, with median marginal bristles. Parafacial usually pruinescent 240

240. Ocellar bristles reclinate (as in Figs. 2–4). Antennal bases separated from one another (as in Fig. 86). Calypter exceptionally large, white, extending over basal third of abdomen (Fig. 217). Apex of female abdomen with pincers-like cerci opposing one another horizontally, each with sharp apex and inner margin armed with peg-like setae (Fig. 249) . . . . **Leucostoma** Meigen, in part[53]

9 spp.; widespread; Reinhard 1956

Ocellar bristles proclinate or absent. Antennal bases contiguous. Calypter not exceptionally large. Abdomen of female without modified pincer-like cerci 241

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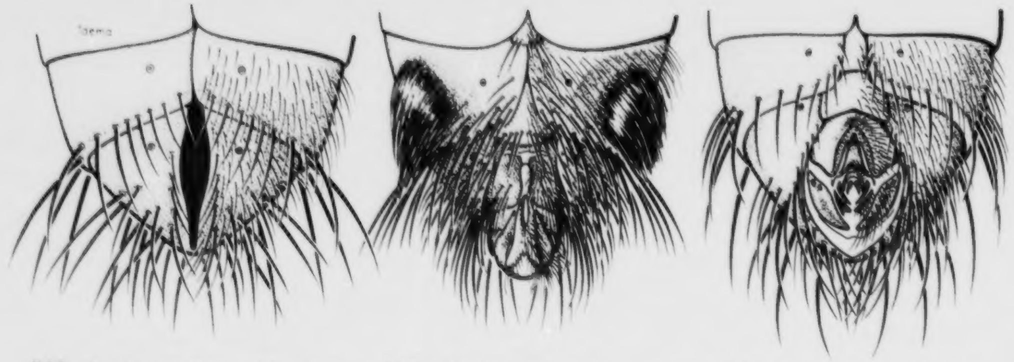
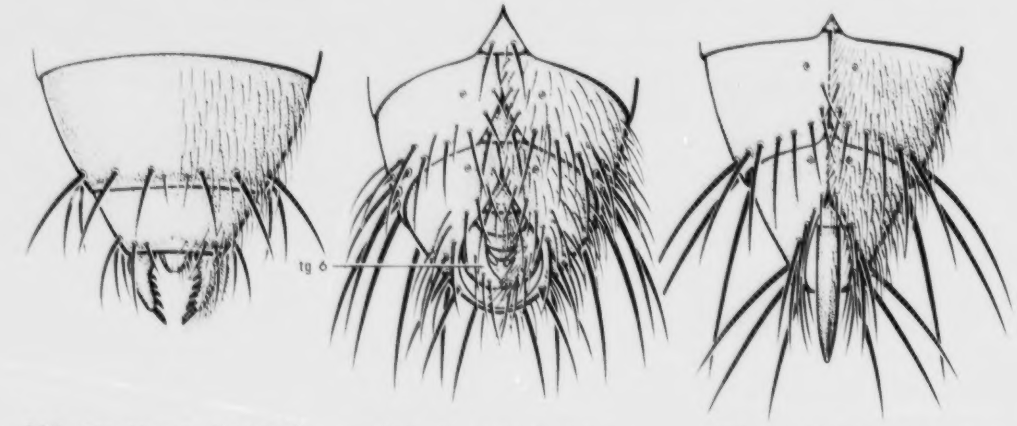
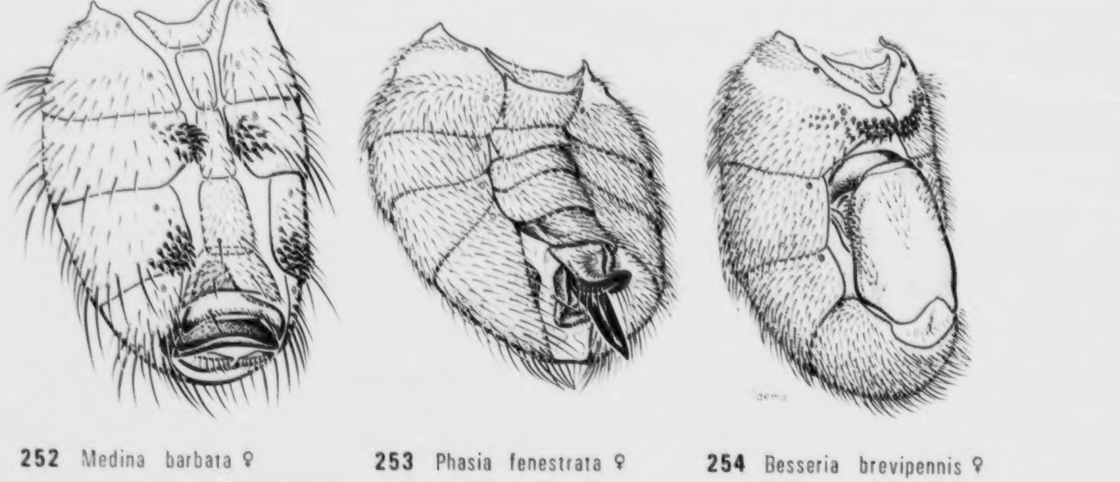
[53] Also included here is *Calyptrosomus dapsilis* Reinhard.



246 Hyphantrophaga blanda ♀ **247** Blepharipa pratensis ♂ **248** Phorocera webberi ♀



249 Leucostoma simplex ♀ **250** Pseudopachystylum debile ♀ **251** Spathidexia clemonsi ♀



252 Medina barbata ♀ **253** Phasia fenestrata ♀ **254** Besseria brevipennis ♀

Figs. 110.246–254. Apices of abdomen: ventral views of (246) *Hyphantrophaga blanda* (Osten Sacken), (247) *Blepharipa pratensis* (Meigen), and (248) *Phorocera webberi* (Smith); (249) dorsal view of *Leucostoma simplex* (Fallén); ventral views of (250) *Pseudopachystylum debile* (Townsend) and (251) *Spathidexia clemonsi* Townsend; oblique ventral view of (252) *Medina barbata* (Coquillett), (253) *Phasia fenestrata* (Bigot), and (254) *Besseria brevipennis* (Loew). Abbreviation: tg, tergite.

241. Second aristomere three or more times as long as wide (Figs. 78, 79, 89) 242

Second aristomere scarcely longer than wide 245

242. First aristomere nearly as long as the second, both of them four or five times as long as wide (Fig. 89). Lower facial margin protruding beyond bases of vibrissae. Acrostichal bristles absent or hair-like ....**Periscepsia** Gistel, in part[54]

8 spp.; widespread; Reinhard 1955 (as *Wagneria*, in part)

First aristomere less than half as long as the second. Lower facial margin not protruding. Acrostichal bristles well-developed..243

243. Parafacial and fronto-orbital plate densely covered with bristles, each arising from a small tubercle (Fig. 78). Arista thickened almost to apex. Third flagellomere of male with basal bulge at point of insertion of arista. Abdominal tergite 3 lacking strongly differentiated median marginal bristles ....**Paradmontia** Coquillett

2 spp.; widespread

Parafacial and fronto-orbital plate less densely covered with bristles, each arising flush with surface (Fig. 79). Arista tapering beyond midpoint to slender apex. Third flagellomere of male not swollen at base. Abdominal tergite 3 with distinct median marginal bristles ... .244

244. Anepimeron bare, except for a single large bristle accompanied by one or two smaller ones at its base...**Mauromyia** Coquillett

2 spp.; widespread in U.S.A.

Anepimeron with a group of small bristles ....**Periscepsia** Gistel, in part

see couplet 242

245. Arista long and slender, of uniform thickness nearly to apex. Parafacial with a single vertical row of strong bristles arising very close to ptilinal fissure (Fig. 85) ....**Hypertrophocera** Townsend[55]

1 sp., *parvipes* Townsend; New Mexico

Arista thickened on basal three-fourths or less. Parafacial not as described 246

246. Abdominal tergites 3 and 4 with median discal bristles (as in Fig. 237).............247

Abdominal tergites 3 and 4 without discal bristles..............................249

247. Prementum slender and elongate, 1.5 times head height, and curved forward (Fig. 110); labella minute, appearing as a continuation of prementum. Abdominal tergite 3 with two pairs of discal bristles, one ahead of the other and set far forward on the segment; hind margin of tergite 2 concave ....**Trochilodes** Coquillett

2 spp.; widespread

Prementum not longer than head height; labella enlarged. Abdominal tergite 3 with a single pair of discal bristles 248

248. Parafacial setae few, small, often only one present, confined to lower fourth of parafacial (as in Fig. 2) ....**Loewia** Egger

1 introduced sp., *foeda* (Meigen); northeastern U.S.A., southern Ontario; Wood and Wheeler 1972

Parafacial setae long and erect, forming a row extending along entire length of parafacial (Fig. 90) ....**Periscepsia** Gistel, in part

see couplet 242

249. Parafacial with scattered short decumbent setae ....**Phyto** Robineau-Desvoidy (see Rhinophoridae, Ch. 109)

Parafacial with row of erect bristles along anterior edge, sometimes flanked with shorter finer hairs (as in Fig. 95)...250

250. Eye setose. Parafacial wider than width of first flagellomere in profile. Wing with long costal spine and dark anterior margin....................**Muscopteryx** Townsend, in part[56]

10 spp.; widespread; Reinhard 1944*a*

Eye bare. Parafacial narrower than width of first flagellomere. Wing with short costal bristle and scarcely any dark pigment...........**Paradidyma** Brauer & Bergenstamm, in part

see couplet 97

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[54] Also included here is *Petinarctia stylata* (Brauer & Bergenstamm).

[55] Included here is *Euthyprosopa petiolata* Townsend.

[56] Included here, in addition to those species treated by Reinhard, are *Tarassophorus evexus* Reinhard and *Websteriana costalis* (Coquillett).

251. M gradually and evenly curved, without an abrupt bend (Fig. 206). Parafacial forming a narrow band encircling lower margin of eye, ending at its posteroventral corner .... **Freraea** Robineau-Desvoidy

1 sp., *montana* (Coquillett); widespread

M with a distinct bend (Figs. 207–214). Parafacial not encircling lower margin of eye, ending before posteroventral part of eye 252

252. Anterior border of postgena rather straight or concave, without pronounced genal dilation, meeting ventral cranial margin behind middle of head; genal groove thus rather extensive (as in Fig. 121) 253

Anterior border of haired part of gena convex anteriorly, curving anteriorly to form a small to moderate genal dilation extending forward to a point anterior to middle of head; genal groove consequently much narrower (as in Figs. 4–6) 260

253. Median surface of fore coxa almost entirely covered with short appressed black setae (as in Fig. 153). Height of eye about half total height of head. Antenna small, recessed into small deep oval facial cavity (Fig. 82). Lower part of face long and narrow, with four or five pairs of large subvibrissal bristles above lower facial margin 254

Median surface of fore coxa with setae confined to anterolateral edge. Height of eye more than half total height of head. Antenna and face not highly modified as above 255

254. Abdomen stout, polished black; tergite 3 usually with more than one pair of median marginal bristles .... **Megaprosopus** Robineau-Desvoidy[57]

1 sp., *regalis* (Reinhard); Arizona

Abdomen less stout, tesselated; tergite 3 with one pair of median marginal bristles .... **Microphthalma** Macquart

4 spp.; widespread; Aldrich 1926*c*

255. Parafacial with a single row of bristles (Fig. 33) .... **Paradidyma** Brauer & Bergenstamm, in part

see couplet 97

Parafacial irregularly covered with setae of varying sizes 256

256. Ultimate section of CuA_1 twice as long as preceding section (Fig. 204); extension of M beyond bend longer than portion of M between crossvein r-m and bend. Parafacial with vertical row of short bristles .... **Goniochaeta** Townsend, in part

see couplet 220

Ultimate section of CuA_1 about equal to or shorter than penultimate section (as in Figs. 207–214) 257

257. Parafacial setae usually of two sizes, namely a single row of larger bristles along anterior margin of parafacial sometimes even arising from membrane anterior to it, flanked by smaller and finer setae laterally (Fig. 92). Integument of body of most species rather shiny, bluish or greenish black. Abdomen more than half as wide as long; tergite 6 and syntergosternite 7 + 8 exposed. Eye facets in male slightly larger on upper two-thirds of eye, and when densely haired, hairs longer above than below .... **Gnadochaeta** Macquart

15 spp.; widespread; Townsend 1915 (as *Myiophasia*)

Parafacial setae not so differentiated into two series. More slender species with narrower gray pruinose, transversely banded abdomen; tergite 6 and syntergosternite 7 + 8 mostly concealed beneath tergite 5. Eye facets not enlarged dorsally in male 258

258. Lower margin of head, when viewed in profile, almost as long as distance from antennal base to back of head; parafacial broad, with uniformly small setulae (Fig. 96). Prementum straight and slender, nearly as long as fore tibia; palpus minute, except in *californicus* (Coquillett) .... **Meledonus** Aldrich[58]

6 spp.; western

Lower margin of head less than two-thirds as long as distance from antennal base to back of head; parafacial with setae increasing in length ventrally (Fig. 93). Prementum less than half as long as fore tibia; palpus variable 259

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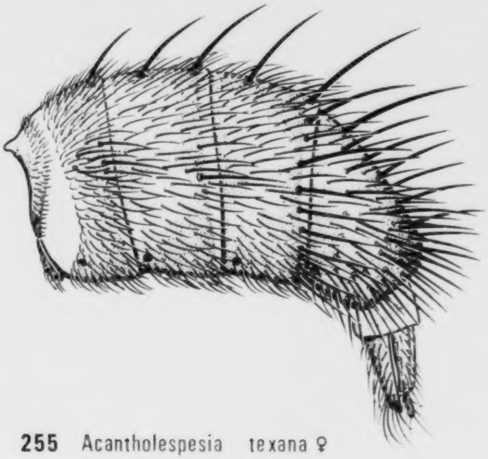
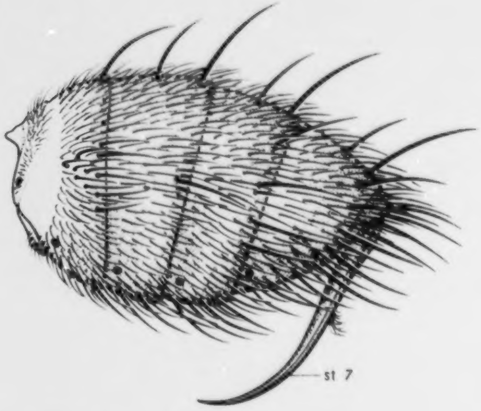
[57] This species was described in the genus *Cochisemyia* Reinhard.

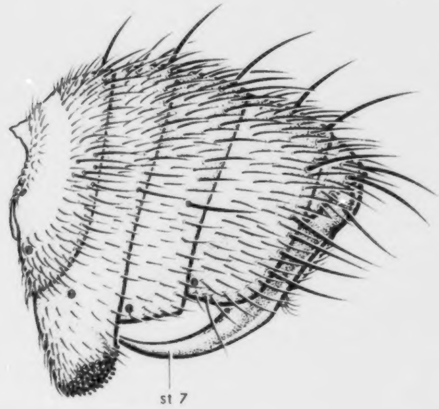
[58] Also included are the species formerly placed in *Athanatus* Reinhard and *Dyscolomyia* Reinhard.



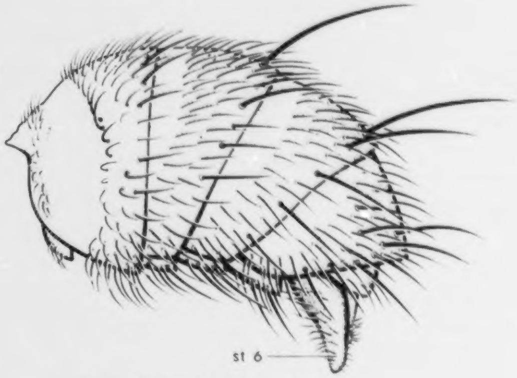
255 Acantholespesia texana ♀



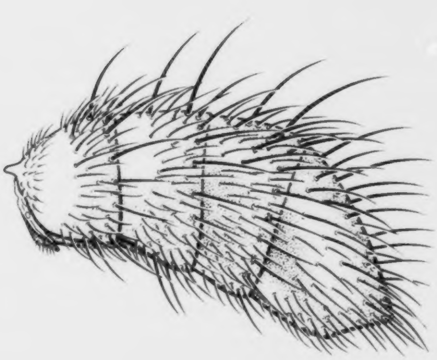
256 Eucelatoria texana ♀



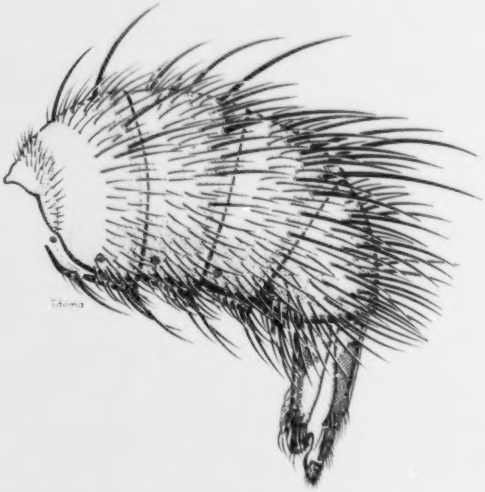
257 Celatoria diabroticae ♀



258 Phyllophilopsis nitens ♀



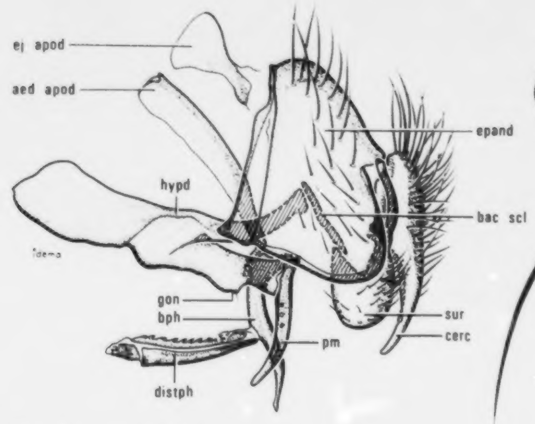
259 Dolichotarsus griseus ♀



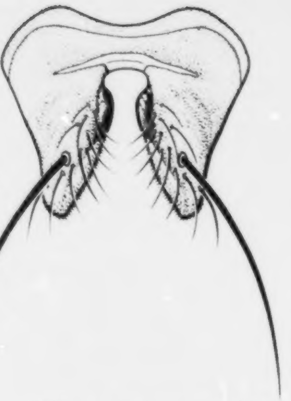
260 Steleoneura novemmaculata ♀

Figs. 110.255–260. Lateral views of abdomen: (255) *Acantholespesia texana* (Aldrich & Webber); (256) *Eucelatoria texana* (Reinhard); (257) *Celatoria diabroticae* (Shimer); (258) *Phyllophilopsis nitens* (Coquillett); (259) *Dolichotarsus griseus* Brooks; (260) *Steleoneura novemmaculata* Wood.

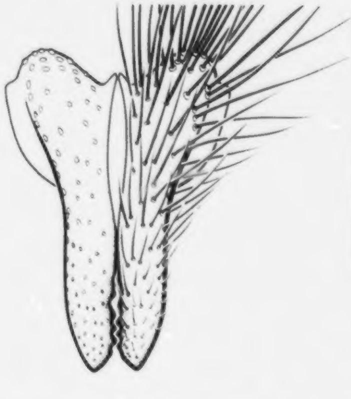
Abbreviation: st, sternite.



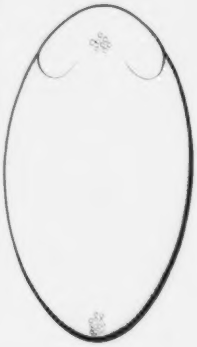
261 Eriothrix penitalis ♂



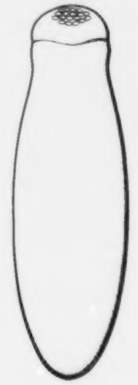
262 Lixophaga variabilis ♂



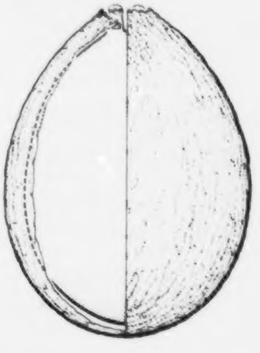
263 Phebellia epicydes ♂



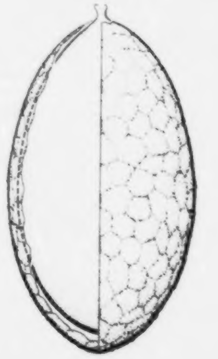
264 Parasetigena silvestris



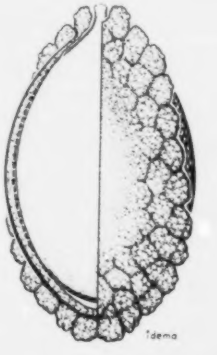
265 Phorocera webberi



266 Euexorista futilis



267 Eumasicera sp.



268 Eumasicera coccidella

Figs. 110.261–268. Male terminalia and eggs: (261) lateral view of left side of male terminalia of *Eriothrix penitalis* (Coquillett); (262) ventral view of sternite 5 of *Lixophaga variabilis* (Coquillett); (263) posterior view of cerci of *Phebellia epicydes* (Walker); dorsal views of egg of (264) *Parasetigena silvestris* (Robineau-Desvoidy) and (265) *Phorocera webberi* (Smith); dorsal views of microtype egg, with portion of dorsal surface removed, of (266) *Euexorista futilis* (Osten Sacken), (267) *Eumasicera* sp., and (268) *Eumasicera coccidella* Townsend.

Abbreviations: aed apod, aedeagal apodeme; bac scl, bacilliform sclerite; bph, basiphallus; cerc, cercus; distph, distiphallus; ej apod, ejaculatory apodeme; epand, epandrium; gon, gonopod; hypd, hypandrium; pm, paramere; sur, surstylus.

259. Anepimeron with one bristle extending back to hind margin of upper calypter. Female with tergite 6 longitudinally divided into two halves (Fig. 250). Male with unhinged aedeagus and well-developed gonopod (as in Figs. 2.138–2.141) .... ***Pseudopachystylum*** Mik

1 sp., *debile* (Townsend); central and eastern

Anepimeron with hairs only. Female with tergite 6 undivided. Male with hinged aedeagus; gonopod reduced (as in Fig. 261) .... ***Phyllomya*** Robineau-Desvoidy[59]

5 spp.; widespread

260. Middorsal depression of abdominal syntergite 1 + 2 extending back to hind margin of that segment (as in Figs. 231, 239); syntergite 1 + 2 lacking median marginal bristles 261

Middorsal depression not extending back to hind margin of syntergite 1 + 2, usually not more than halfway back; syntergite 1 + 2 with median marginal bristles and sometimes with median discal bristles as well 265

261. Palpus greatly reduced, parallel-sided, usually shorter than pedicel (Fig. 101) .... ***Linnaemya*** Robineau-Desvoidy, in part[60]

8 spp.; widespread; Brooks 1944*b* (as several genera)

Palpus clavate, normal in length, longer than pedicel 262

262. Bristles on lower part of parafacial reclinate, curved dorsally, forming an evenly spaced row that is continuous with frontal bristle row, and evidently an extension of it extending ventrally nearly to lower margin of parafacial (Fig. 104). First flagellomere of male sometimes divided longitudinally into two or three branches (Fig. 2.45) .... ***Dichocera*** Williston, in part[61]

7 spp.; widespread

Bristles on lower part of parafacial proclinate, curved ventrally, separated from reclinate lowermost bristle of frontal row at level of insertion of arista 263

263. Aristomeres 1 and 2 elongate, all three subequal in length (Fig. 132). R_1 and R_{4+5} each setose dorsally along most of their length .... ***Triarthria*** Stevens

1 introduced sp., *spinipennis* (Meigen); west coast, Newfoundland, Massachusetts

Aristomeres 1 and 2 scarcely longer than wide, much shorter than aristomere 3. R_1 bare and R_{4+5} setose only at base, or bare 264

264. Antennal bases widely separated by low facial carina (Fig. 86). Parafacial with fine hairs only. Antenna dark .... ***Ursophyto*** Aldrich

1 sp., *nigriceps* (Bigot); western

Antennal bases contiguous or nearly so, and face without median carina. Parafacial with some bristles on lower part, as well as hairs. Antenna orange .... ***Lypha*** Robineau-Desvoidy, in part

see couplet 104

265. Wing patterned as in Fig. 210; bend of M extremely obtuse. Integument yellowish, translucent .... ***Chiricahuia*** Townsend

1 sp., *cavicola* Townsend; Arizona

Wing unpatterned, transparent; bend of M more acute. Integument dark brown or black, opaque 266

266. Parafacial with a single evenly spaced row of long, stout setae, increasing in size ventrally, usually also with some shorter finer hairs laterally (Fig. 95) 267

Parafacial with scattered setae not arranged in a row 269

267. Aristomere 2 three or more times as long as wide; aristomere 1 also longer than wide (as in Fig. 135). Subvibrissal ridge entirely separated from genal dilation by a branch of genal groove that extends ventrally to subcranial margin and is continuous with membrane supporting proboscis (as in Figs. 118, 142). Scutellum with long nearly equal lateral and subapical bristles as well as minute apical bristles (as in Fig. 185, except that lateral and subapical bristles more parallel to each other, and apicals smaller) .... ***Coloradomyia*** Arnaud

1 sp., *eucosmaphaga* Arnaud; Colorado, Utah

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[59] Included here are all species placed in *Gibsonomyia* Curran, *Pseudomorinia* Wulp, and *Dexia sensu* Sabrosky and Arnaud (1965: 1021) not Meigen.

[60] Also included are all species formerly assigned to *Bonnetia* Robineau-Desvoidy, *Nigrobonellia* Brooks, and *Thompsonomyia* Brooks.

[61] Also included are all species formerly placed in *Cacozelus* Reinhard, *Metamyia* Arnaud, and *Neodichocera* Walton; *orientalis* (Coquillett) and *tridens* Walton are distinct species and Fig. 2.45 is of the latter species.

Aristomere 2 no more than twice as long as wide (as in Figs. 126, 128). Aristomere 1 minute. Subvibrissal ridge and genal dilation forming a continuous sclerite, only partially divided by a branch of genal dilation, and subvibrissal ridge with single even row of bristles extending back along lower cranial margin of postgena. Scutellum with long divergent lateral bristles and moderately long crossed apical bristles (as in Fig. 183) 268

268. Aristomere 3 strongly swollen only on basal fourth or less, tapering abruptly to apex (as in Fig. 118). First flagellomere no longer than 1.5 times length of pedicel. Vibrissa arising above level of lower facial margin .... ***Muscopteryx***, in part
see couplet 250

Aristomere 3 thickened on basal third or more before tapering to apex. First flagellomere two or more times length of pedicel. Vibrissa arising at level of lower facial margin .... ***Blepharomyia*** Townsend[62]
3 spp.; widespread

269. Eye with short sparse hairs; each hair no longer than combined diameter of two or three facets .... ***Goniocera*** Brauer & Bergenstamm
1 sp., *io* (Aldrich); eastern

Eye densely covered with conspicuous long hairs 270

270. Pedicel with dense patch of stout erect bristles, each about as long as width of pedicel at point of attachment (Fig. 97). Longest parafacial hairs more than half as long as arista...... .... ***Metopomuscopteryx*** Townsend
3 spp.; western

Pedicel with few, sparse hairs and one or two bristles, most shorter than width of pedicel (Fig. 94). Parafacial hairs at most less than one-third as long as arista .... ***Macquartia*** Robineau-Desvoidy, in part[63]
4 spp.; Canada and Alaska

271. Scutum without bristles except for one pair of each of the following: presutural supra-alar, posteriormost presutural dorsocentral, postsutural supra-alar, postsutural intra-alar, postsutural dorsocentral, and postsutural acrostichal; usually only one katepisternal bristle present, in posterodorsal corner (Fig. 171). Abdominal tergites without dorsal bristles 272

Scutum with two or more additional pairs of postsutural supra-alar, dorsocentral, and acrostichal bristles; katepisternum with two or more bristles (as in Figs. 172–178). Abdominal tergites usually with at least one pair of marginal bristles 276

272. Hind tibia with dorsal longitudinal row of long flattened blade-like setae, each as long as width of tibia at its point of attachment, flanked by a second row of similarly shaped but much shorter setae (Fig. 224) .... ***Trichopoda*** Berthold
6 spp.; widespread

Hind tibia lacking rows of long flattened setae 273

273. Palpus minute, much shorter than pedicel (as in Fig. 96). Abdomen orange red without dark markings, convex dorsally, twice as long as wide, and covered with prominent recumbent black hairs, none of which is enlarged or bristle-like; apex of abdomen of female folded ventrally; ventral edges of tergite 2 studded with spine-like setae (Fig. 254) .... ***Besseria*** Robineau-Desvoidy, in part[64]
3 spp.; widespread

Palpus well-developed, longer than pedicel and usually longer than antenna. Abdomen, if orange red, with dark markings; apex of abdomen of female not folded ventrally and not opposed by spine-like setae on ventral side of tergite 2 274

274. Abdomen flattened dorsally, distinctly longer than wide, usually dark colored, but if pale in ground color, then densely pruinose .... ***Phasia*** Latreille[65]
24 spp.; widespread; Brooks 1945*b*, as several genera

Abdomen hemispherical dorsally, scarcely longer than wide, orange red in ground color, usually with dorsal dark markings, sometimes almost black in female 275

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[62] Included here are those species formerly assigned to *Ictericophyto* Townsend.

[63] Included here are those species formerly assigned to *Alaskophyto* Townsend and *Myioclonia* Reinhard.

[64] Also included here are the species formerly placed in *Apinops* Coquillett and *Apostrophus* Loew.

[65] Also included here are the species formerly placed in *Alophorella* Townsend, *Hyalomya* Robineau-Desvoidy, *Paraphorantha* Townsend, *Phasiomyia* Townsend, and *Phoranthella* Brooks.

275. Apex of scutellum without bristles; apical pair so widely separated and short that they appear as lateral bristles and cannot cross at their apices. Abdomen shiny, orange red with black markings, or sometimes entirely black, with short hairs each arising from a raised base, giving abdomen a somewhat rugose appearance. Pedicel and first flagellomere in most species elongate, extending to level of vibrissa (Fig. 87) .... ***Gymnosoma*** Meigen[66]

6 spp.; widespread; Brooks 1946, in part (as several genera)

Apex of scutellum with the usual crossed pair of apical bristles (as in Fig. 190). Abdomen usually golden tomentose (in male) or gray tomentose (in female); intertergal sutures distinct. Pedicel and first flagellomere short, not extending to level of vibrissa (Fig. 88) .... ***Gymnoclytia*** Brauer & Bergenstamm

6 spp.; widespread; Brooks 1946, in part (as several genera)

276. Postmetacoxal area sclerotized, i.e. posterior edges of metepimera extending posteromedially to meet each other at midline between hind coxae and base of first abdominal sternite, forming a postmetacoxal bridge (Fig. 230) 277

Postmetacoxal area membranous, distinctly paler in color than adjacent metepimera 279

277. Hind margin of eye indented (as in Fig. 111). Ocellar triangle extending forward to lunule as a polished brown strap-like sclerite (Fig. 58) .... ***Hemyda*** Robineau-Desvoidy

1 sp., *aurata* Robineau-Desvoidy; widespread

Hind margin of eye straight or evenly convex. Ocellar triangle normal in shape, not dividing frontal vitta 278

278. Palpus present. Vibrissae arising distinctly above lower margin of face. Legs yellowish basally, darkened apically .... ***Xanthomelanodes*** Townsend

5 spp.; widespread

Palpus absent. Vibrissae level with lower margin of face. Legs entirely dark .... ***Cylindromyia*** Meigen[67]

18 spp.; widespread; Aldrich 1926*b*

279. M ending in R_{4+5} well before wing margin (Figs. 211, 212) 280

M ending in wing margin or in R_{4+5} near margin (Figs. 213, 214) 290

280. Ocellar bristles lateroclinate or slightly reclinate (as in Fig. 108). Calypter usually white, exceptionally large, extending beyond middle of syntergite 1 + 2 (Fig. 217). Apex of female abdomen with pincers-like cerci, each with sharp apex and peg-like setae on inner margin (Fig. 249) .... ***Leucostoma*** Meigen, in part

see couplet 240

Ocellar bristles proclinate or absent. Calypter not extending back to middle of syntergite 1 + 2. Apex of female without pincers-like cerci (except in *Cinochira* and *Clairvillia*) 281

281. Wing slender, usually darkened with whitish apex. M beyond bend meeting R_{4+5} at right angles; R_{4+5} + M twice as long as portion of M beyond bend (Fig. 211) .... ***Catharosia*** Rondani[68]

5 spp.; widespread

Wing not as described above; M not so abruptly bent anteriorly 282

282. Large species, over 10 mm in length, slender, black, pepsid-like, with entirely black wings. Facial ridge with recumbent hairs (Fig. 98); upper part of parafacial with several medioclinate setae .... ***Penthosia*** Wulp

1 sp., *satanica* (Bigot); Arizona, Mexico

Smaller species, not entirely black with black wings, not resembling a pepsid wasp 283

283. Wing patterned with brown spots, bars, and triangles (Figs. 212, 214) 284

Wing transparent, unpatterned 285

284. Face with prominent oval central tubercle or carina (Fig. 122). Antenna long, cylindrical; pedicel and first flagellomere each as long as arista. Lunule without setae. Thorax black. Apex of cell r_{4+5} dark (Fig. 212) .... ***Euthera*** Loew

3 spp.; widespread; Brooks 1945*a*

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[66] Also included here is *amplifrons* (Brooks), placed in *Cistogaster* Latreille by Sabrosky and Arnaud (1965).

[67] Also included here is *Ichneumonops mirabilis* Townsend.

[68] Also included here are the species formerly placed in *Procatharosia* Villeneuve.

Face with at most a low indistinct keel-like carina between antennae. Antenna short; length of pedicel and first flagellomere together no longer than arista. Lunule, in some species, with setulae (Fig. 59). Thorax yellow or pale brown. Apex of cell r_{4+5} transparent (Fig. 214) .... ***Oestrophasia*** Brauer & Bergenstamm[69]
4 spp.; widespread

285. Proboscis extremely long and slender, curving forward, longer than height of head (Fig. 112). Face pruinose, with thickened flat-topped carina separating very short antennae. Tergite 7 of female divided medially into two spine-covered lobes .... ***Imitomyia*** Townsend
1 sp., *sugens* (Loew); central and western

Proboscis not exceptionally long, shorter than height of head. Face without a prominent carina. Tergite 7 of female abdomen without spine-covered lobes 286

286. Eye very large, occupying almost all of side of head; gena reduced to a narrow band less than one-tenth height of head (Fig. 99) .... ***Strongygaster*** Macquart, in part[70]
4 spp.; widespread; Brooks 1942 (as *Clistomorpha*)

Gena much wider, one-sixth height of head or more 287

287. Eye covered with conspicuous dense hair. Facial ridge with setae on lower two-thirds or more; the uppermost of these setae situated at level of lowest frontal bristles; frontal bristles extending ventrally below level of base of arista (Fig. 100) .... ***Mactomyia*** Reinhard
1 sp., *fracida* Reinhard; western

Eye bare. Setae of facial ridge, if present, well below level of lowest frontal bristle; frontal bristles not descending to level of base of arista 288

288. Inner vertical bristles long and stout, more than two-thirds as long as height of eye (Fig. 107) .... ***Vanderwulpia*** Townsend[71]
2 spp.; southwestern

Inner vertical bristles much less than one-fourth as long as height of eye, or absent ... 289

289. Antennae separated at base by a distance at least equal to width of scape (as in Figs. 80, 86). All abdominal setae rather weak and uniform in size, not distinctly differentiated into bristles and hairs .... ***Rondania*** Robineau-Desvoidy
1 sp., *dimidiata* (Meigen); Alaska, northwestern Canada

Antennae contiguous at base. Abdominal setae distinctly differentiated into marginal and discal bristles and much shorter hairs; these hairs no longer than one-third the length of the bristles .... ***Clastoneuriopsis*** Reinhard, in part
see couplet 117

290. Eye almost entirely covered with long hairs 291

Eye apparently bare 308

291. Ocellar bristles posterolaterally inclined (Fig. 108); facial ridge with row of stout erect evenly spaced bristles. Proepisternum with pale hairs (as in Fig. 166) .... ***Campylochaeta*** Robineau-Desvoidy
11 spp.; widespread; Reinhard 1952, Sabrosky 1975 (as *Chaetophlepsis*)

Ocellar bristles proclinate or absent; facial ridge bare or with recumbent setae on lower half. Proepisternum bare 292

292. Palpus reduced, parallel-sided, usually shorter than pedicel (Fig. 101) .... ***Linnaemya*** Robineau-Desvoidy, in part
see couplet 261

Palpus clavate, normal in length, longer than pedicel 293

293. Body and most of head metallic green or blue .... ***Gymnocheta*** Robineau-Desvoidy, in part
see couplet 7

Body and head yellowish brown or black, not metallic green 294

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[69] Also included here are the species formerly placed in *Cenosoma* Wulp.

[70] Included here are all species formerly placed in *Clistomorpha* Townsend and *Hyalomyodes* Townsend.

[71] Also included here are the species formerly placed in *Catemophrys* Townsend.

294. Middle basal bristle of postpronotum displaced anterolaterally, arising between anterior bristle and outer basal bristle or lateral to a line between them, and forming a nearly right-angled triangle with outer and inner basal bristles (as in Figs. 157, 159) 295

Middle basal bristle of postpronotum in line with outer and inner basal bristles (as in Figs. 158, 160) 299

295. Face convex, visible in profile; lower margin protruding anterior to vibrissal angle (Fig. 102) 296

Face flat or deeply concave; neither central part nor lower margin visible in profile 297

296. Scutellum with three or more pairs (basal, lateral, and subapical) of divergent bristles, and usually also with a small pair of crossed apical bristles (as in Fig. 185) .... ***Panzeria*** Robineau-Desvoidy[72]

28 spp.; widespread; Tothill 1921 (as *Ernestia*), Brooks 1943 (as several genera)

Scutellum with only two pairs (basal and subapical) of scutellar bristles, both pairs divergent (as in Fig. 186) .... ***Neosolieria*** Townsend

1 sp., *sila* (Reinhard); California, Utah

297. Abdominal tergite 5 orange, contrasting with dark preceding tergites; tergites 3 and 4 each with two pairs of discal bristles, with one pair anterior to the other (as in Figs. 235, 239) .... ***Hineomyia*** Townsend

1 sp., *setigera* (Coquillett); eastern

Abdominal tergites concolorous: tergites 3 and 4 each with one pair of discal bristles or none 298

298. Large species, over 8 mm, shiny black or dark reddish brown, with yellow upper and lower calypteres and wing base. Antenna black .... ***Melanophrys*** Williston[73]

2 spp.; widespread

Small species, less than 6 mm, grayish brown to blackish, pruinose, with white calypteres and wing base. Antenna orange .... ***Hyalurgus*** Brauer & Bergenstamm[74]

2 spp.; central and eastern

299. Anepimeral bristle well-developed, extending back well beyond middle of lower calypter (Fig. 216) 300

Anepimeral bristle shorter, not extending to middle of lower calypter 303

300. Arista thickened nearly to apex (as in Figs. 127, 128) 301

Arista thickened on less than basal half, tapering before middle to long thread-like apex 302

301. Frontal bristles extending ventrally, in an evenly spaced row, nearly to lower margin of parafacial (Fig. 104). First flagellomere of male sometimes divided longitudinally into two or three branches (Fig. 2.45) .... ***Dichocera*** Williston, in part

see couplet 262

Frontal bristles extending ventrally only to level of base of first flagellomere (as in Fig. 105); parafacial with a few hairs below lowest frontal bristle. Antenna of male undivided .... ***Ostracophyto*** Townsend

1 sp., *aristalis* Townsend

302. Vibrissae arising distinctly above level of lower facial margin; facial margin protruding forward, visible in lateral view (Fig. 106) .... ***Spilochaetosoma*** Smith

1 sp., *californicum* Smith; western

Vibrissae arising at same level as lower margin of face; facial margin not visible in lateral view .... return to 104

303. Middorsal depression on abdominal syntergite 1 + 2 extending back to hind margin of syntergite (as in Fig. 231) 304

Middorsal depression scarcely extending back beyond middle of syntergite 306

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[72] Included here are all species formerly placed by Sabrosky and Arnaud (1965) in *Appendicia* Stein, *Melinocera* Townsend, *Mericia* Robineau-Desvoidy, *Metaphyto* Coquillett, *Promericia* Brooks, and *Pseudomeriana* Brooks—almost all the members of the tribe Ernestiini. Although *Ernestia* Robineau-Desvoidy is a more familiar generic name, this name was synonymized with *Panzeria* by Robineau-Desvoidy himself. Relationships with Palaearctic species now placed in *Ernestia*, *Eurithia* Robineau-Desvoidy, and *Fausta* Robineau-Desvoidy remain to be ascertained.

[73] Included here is *Atropharista insolita* (Walker).

[74] Included here are the species formerly placed in *Xanthocera* Townsend.

304. Anterior and posterior lappets of posterior thoracic spiracle nearly equal in size; each lappet composed of a row of plumose hair-like extensions (as in Fig. 169). Lower margin of face not protruding beyond vibrissal angle .... ***Uramya*** Robineau-Desvoidy[75]
7 spp.; widespread

Anterior and posterior lappets unequal in size; posterior lappet subcircular (as in Fig. 170). Lower margin of face protruding well beyond vibrissal angle (Fig. 116) 305

305. Distance between eye and lower cranial margin three or more times width of parafacial (Fig. 116). Arista strongly thickened on at least basal third. Palpus slender, not abruptly clubbed. Ocellar setae of female, and of both sexes of *arctica* (Sack), lateroclinate .... ***Trafoia*** Brauer & Bergenstamm[76]
2 spp.; widespread

Distance between eye and lower cranial margin about equal to width of parafacial. Arista slender, even at base. Palpus clubbed apically. Ocellar setae of female proclinate .... ***Eriothrix*** Meigen
1 sp., *penitalis* (Coquillett); eastern

306. Base of R_{4+5} without setae, dorsally or ventrally. Scutellum with lateral, subapical, and apical bristles all more or less equivalent in size; apical bristles parallel or divergent (Fig. 189). Antennal axis of head 1.5 times that of vibrissal axis (Fig. 118) .... ***Cleonice*** Robineau-Desvoidy[77]
3 spp.; widespread

Base of R_{4+5} with setae both dorsally and ventrally. Scutellum with stout divergent lateral bristles, short weak subapical bristles, and stout crossed apical bristles. Antennal axis of head less than 1.5 times that of vibrissal axis 307

307. Genal groove relatively large, triangular, formed by separation of parafacial and genal dilation from vibrissal angle (Fig. 94). Eye height about two-thirds height of head. Three postsutural intra-alar bristles present .... ***Macquartia*** Robineau-Desvoidy, in part
see couplet 270

Genal groove nearly obliterated by the meeting of genal dilation, parafacial, and vibrissal angle (Fig. 119). Eye height about four-fifths height of head. Two postsutural intra-alar bristles present .... ***Dufouria*** Robineau-Desvoidy
1 sp., *americana* (Reinhard); Ohio, Northwest Territories

308. Palpus minute, shorter than pedicel, or absent 309

Palpus well-developed, longer than pedicel 312

309. Hind margin of eye indented (Fig. 111). Prementum slender, elongate, more than twice as long as height of head. Abdomen orange red, slender, contrasting with dark wings .... ***Beskia*** Brauer & Bergenstamm
1 sp., *aelops* (Walker); southern

Hind margin of eye straight or evenly convex. Prementum shorter than height of head. Abdomen and wings not as above 310

310. Larger species, 10 mm or more in length. Head and body mostly yellowish or pale brownish pruinescent. Abdomen slender, pointed apically. Apical scutellar bristles about half as long as subapical scutellar bristles; lateral scutellar bristles undeveloped .... ***Ervia*** Robineau-Desvoidy
1 sp., *triquetra* (Olivier); eastern U.S.A.

Smaller species, under 7 mm in length. Head and body mostly black or gray. Abdomen black. Apical scutellar bristles as long as lateral scutellar bristles; subapical scutellar bristles reduced (as in Fig. 181) 311

311. Abdominal sternites unsclerotized; edges of tergites widely separated midventrally, connected by pale membrane, with terminalia tucked into resulting cavity (Fig. 254); intersegmental junction between tergites 4 and 5 more prominent than between tergites 2 and 3 or tergites 3 and 4. Cell r_{4+5} opening at apex of wing (as in Fig. 199) .... ***Besseria*** Robineau-Desvoidy, in part
see couplet 273

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[75] Included here are all species included by Sabrosky and Arnaud (1965) in the tribe Uramyiini, *viz. Anaporia* Townsend, *Paraporia* Townsend (mistakenly regarded as Nearctic), *Pseudeuantha* Townsend, and *Uramya* Robineau-Desvoidy. *U. aldrichi* Reinhard, although not considered as occurring north of Mexico, evidently occurs in Arizona and Texas.

[76] Also included here is *Tenuirostra arctica* (Sack).

[77] Included here are all species formerly placed in *Grisdalemyia* Curran.

Abdominal sternites fully sclerotized; connecting edges of tergites with little or no membrane exposed; intersegmental junctions between tergites 2–5 all equally well-defined. Cell r_{4+5} ending before apex of wing .... ***Pseudapinops*** Coquillett
2 spp.; widespread

312. Ocellar setae inclined laterally or posterolaterally (as in Fig. 108) 313
Ocellar setae proclinate or absent 314

313. Proboscis long and slender (as in Figs. 110–112). Frons (at antennal bases) and lower facial margin prominent in lateral view. Cerci of female minute, unmodified .... ***Evidomyia*** Reinhard
1 sp., *infida* Reinhard; California

Proboscis no longer than height of head. Frons not prominent and lower facial margin scarcely visible in lateral view. Cerci of female strongly sclerotized, forming a pincers-like organ for grasping host (as in Fig. 249) .... ***Clairvillia*** Robineau-Desvoidy
3 spp.; western

314. M nearly straight, extending to wing margin without an abrupt bend (thus resembling a muscid or acalyptrate, as in Fig. 206). Abdomen of female long, slender, and tapering; cerci forming a pincers-like organ for grasping host (as in *Leucostoma* and *Clairvillia*, Fig. 249) .... ***Cinochira*** Zetterstedt
1 sp., *mitis* (Reinhard); Texas

M with a distinct angular bend. Abdomen broader; female without pincers-like organ for grasping host 315

315. Medial surface of fore coxa entirely covered with appressed setulae (as in Fig. 153) ...... ***Thelaira*** Robineau-Desvoidy
2 spp.; widespread

Medial surface of fore coxa bare (as in Figs. 154, 155); appressed setulae confined to anteromedial surface with bare area medially 316

316. Lower proepimeral bristle well-developed, directed anteroventrally, in opposite direction to upper proepimeral bristle (Fig. 167)......................... ***Neaera*** Robineau-Desvoidy[78]
4 spp.; central and eastern U.S.A.

Lower proepimeral bristle absent, or reduced in size and directed dorsally, parallel to upper proepimeral (as in Fig. 166) 317

317. M not reaching wing margin, ending about where bend should be (Fig. 4.74) 318
M reaching wing margin, with bend in usual position 319

318. Facial ridge and vibrissal angle exceptionally prominent, extending forward as a fold or flange (Fig. 109); facial ridge with an irregular row of short decumbent setulae............. ***Bezzimyia*** Townsend
1 sp., *americana* (Curran); southern

Facial ridge bare; vibrissal angle not exceptionally prominent .... ***Besseria*** Robineau-Desvoidy, in part
see couplet 273

319. Vibrissa not distinctly differentiated; genal groove exceptionally large; postgenal margin rather straight and vertical, ending below eye (Fig. 121) 320
Vibrissa distinctly differentiated (as in Fig. 120); postgenal margin extending forward below eye forming a distinct genal dilation (as in Figs. 122–124)..................... 321

320. Katepisternum with two bristles; in some specimens a small third bristle present anterior to anteriormost large bristle (Fig. 172); two postsutural supra-alar bristles present .... ***Eutrixa*** Coquillett
2 spp.; widespread

Katepisternum with only one bristle (as in Fig. 171); three postsutural supra-alar bristles present .... ***Isidotus*** Reinhard
1 sp., *incanus* Reinhard; Arizona

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[78] Included here is *Acronarista mirabilis* Townsend, and the species formerly placed in *Acronaristopsis* Townsend, *Dichaetoneura* Johnson, and *Euryceromyia* Townsend.

321. Prosternum inflated (Fig. 155) .... ***Ormia*** Robineau-Desvoidy

7 spp.; widespread, U.S.A., southern Canada; Sabrosky 1953*a*, 1953*b* (as *Ormia* and *Euphasiopteryx* Townsend)

Prosternum normal 322

322. Face convex, visible in lateral view, at least on lower half (Figs. 114, 115, 120) 323

Face concave at least on upper half, not visible in profile except sometimes at vibrissal angle 329

323. Mid tibia with only one anterodorsal bristle or none (as in Fig. 221) 324

Mid tibia with two or more anterodorsal bristles (as in Fig. 222) 327

324. Pleuron with dense tufts of long white plumose hairs (Fig. 168) ..... ***Leskiopsis*** Townsend

1 sp., *thecata* (Coquillett); eastern U.S.A.

Pleural hairs not plumose and not especially long or dense 325

325. R_{4+5} setose more than halfway to crossvein r-m (as in Fig. 199). Postpronotum with a small anterolateral bristle in addition to the basal bristles (Fig. 161) .... ***Genea*** Rondani[79]

7 spp.; widespread; James 1947 (as several genera)

R_{4+5} with a few setae at base only. Postpronotum lacking an anterolateral bristle (as in Fig. 160) 326

326. Mid tibia with one anterodorsal bristle .... ***Leskia*** Robineau Desvoidy[80]

3 spp.; widespread

Mid tibia without an anterodorsal bristle .... ***Drepanoglossa*** Townsend[81]

2 spp.; western

327. Arista short plumose along its entire length; longest hairs longer than greatest width of arista (as in Figs. 125, 134) .... ***Trochiloleskia*** Townsend

1 sp., *loriola* (Reinhard); southern Texas

Arista bare, or nearly so; the longest hairs shorter than width of arista (Fig. 133) 328

328. Arista thickened on basal two-thirds or more, tapering abruptly to slender apex (Fig. 133). Prementum longer than fore femur .... ***Aphria*** Robineau-Desvoidy

2 spp.; widespread

Arista thickened on less than basal half, tapering gradually and uniformly to apex (Fig. 134). Prementum shorter than fore femur .... ***Solieria*** Robineau-Desvoidy[82]

5 spp.; widespread

329. Prementum long and slender, often curved posteriorly, at least as long as height of eye, and in most species longer than height of head (Figs. 113–115); labella minute, pointed, scarcely wider than apex of prementum 330

Prementum shorter than height of eye; labella normal, pad-like 332

330. Posterior margin of eye slightly concave (Fig. 114). Antenna arising near level of middle of eye; first flagellomere no longer than half height of eye. Scutellum with well-developed lateral bristles (as in Fig. 179) .... ***Epigrimyia*** Townsend

2 spp.; central and eastern U.S.A.

Posterior margin of eye convex (Figs. 113, 115). Antenna arising near upper margin of eye; first flagellomere large in both sexes, as long as height of eye. Scutellum lacking lateral bristles (as in Fig. 186) 331

331. Membrane between lower facial margin and clypeus with a pair of convex subtriangular sclerites (as in Fig. 152). Aristomere 2 elongate, two or more times as long as wide; first flagellomere truncate, widest beyond middle (Fig. 113) .... ***Clausicella*** Rondani[83]

8 spp.; widespread; Reinhard 1946*c* (as *Siphophyto*)

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[79] Also included are all species formerly assigned to *Dejeaniopalpus* Townsend, *Jaynsleskia* Townsend, *Leskiella* James, *Leskiomima* Brauer & Bergenstamm, and *Siphoclytia*, including *pavonacea* (Reinhard).

[80] Included here are all species formerly assigned to *Eumyobia* Townsend, *Myobiopsis* Townsend, and *Sipholeskia* Townsend.

[81] Also included is *Philocalia tenuirostris* Reinhard.

[82] Included here is *Solieriopsis boreotis* Reinhard, and, provisionally, the species included in *Apachemyia* Townsend, *Neofischeria* Townsend, *Parademoticus* Townsend, and *Parafischeria* Townsend. Although the four latter species might better be placed in *Demoticus* Macquart, no ready distinction between the genera seems possible, and a study of world genera of the tribe Aphriini is needed.

[83] Also included here are the species formerly placed in *Coronimyia* Townsend.

Membrane between lower facial margin and clypeus without above-mentioned such sclerites. Aristomere 2 minute, no longer than wide; first flagellomere rounded apically, widest before middle (Fig. 115) . . . . ***Crocinosoma*** Reinhard

1 sp., *cornuale* Reinhard; southern

332. Arista plumose, with the longest hairs longer than greatest width of arista (as in Figs. 64, 125, 134) 333

Arista bare, or nearly so, with the longest hairs shorter than greatest width of arista 336

333. Aristal hairs much longer at base of arista than at apex, arising all around arista (as in Fig. 64). Parafacial with minute pale hairs. Midleg of male about twice as long as foreleg or hindleg . . . . ***Cholomyia*** Bigot

1 sp., *inaequipes* Bigot; eastern and southwestern U.S.A.

Aristal hairs as long at apex of arista as on base (as in Figs. 125, 134). Parafacial bare. Midleg of male not exceptionally long 334

334. Genal dilation extending anteriorly to vibrissal angle and parafacial, reducing genal groove to a sulcus (Fig. 146). Small shiny brown species with little pale pruinosity . . . . ***Anthomyiopsis*** Townsend

1 sp., *cypseloides* Townsend; northern

Genal dilation separated from vibrissal angle and parafacial by a distinct triangular pruinose genal groove. Species with extensive pale pruinose areas 335

335. Scutellum with well-developed lateral bristles in addition to basal and apical bristles (as in Fig. 183, except that lateral bristles are parallel or convergent). R_{4+5} setose at least to cross-vein r-m. Facial ridge usually with a few pale hairs above vibrissa. Female with sword-like ovipositor protruding from apex of abdomen (Fig. 251), except in *elegans* (Reinhard) . . . . ***Spathidexia*** Townsend[84]

7 spp.; widespread; Arnaud 1960, in part

Scutellum with well-developed basal and apical bristles only; lateral setae hair-like (as in Fig. 186). R_{4+5} with one bristle at base. Facial ridge without pale hairs. Ovipositor tubular . . . . ***Chaetonopsis*** Townsend

1 sp., *spinosa* (Coquillett); central and eastern U.S.A.

336. Scutum with only one pair of presutural acrostichal bristles, the posteriormost pair, which is situated anterior to scutellum 337

Scutum usually with two pairs of presutural and two pairs of postsutural acrostichal bristles 338

337. Scutellum without well-developed lateral bristles. Back of head convex . . . . ***Euclytia*** Townsend

1 sp., *flava* (Townsend); widespread

Scutellum with well-developed lateral bristles as well as basal and apical bristles. Upper third or more of back of head concave (Fig. 61) . . . . ***Opesia*** Robineau-Desvoidy

1 sp., *atrata* (Coquillett); northern

338. Eye, viewed in profile, occupying almost entire side of head, more than half as long (front to back) as high, thus reducing parafacial and gena to narrow bands (Fig. 99) . . . . ***Strongygaster*** Macquart, in part

see couplet 286

Eye, viewed in profile, less than half as long (front to back) as high; parafacial, gena, and postgena more extensive (Figs. 46, 49) 339

339. Lateral scutellar bristles lacking (Fig. 186) 340

Lateral scutellar bristles well-developed (as in Figs. 184, 185) 342

340. Mid tibia without a ventral bristle. Abdominal sternite 7 of female a sharp slightly curved piercer sheathed in a spout-like sternite 6 (Fig. 258) . . . . ***Phyllophilopsis*** Townsend, in part

see couplet 148

Mid tibia with well-developed ventral bristle. Ovipositor tubular, without piercer 341

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[84] Also included here, in addition to those treated by Arnaud, are the species placed in *Gymnopalpus*, including *elegans* (Reinhard), described in the genus *Minthodexiopsis* Townsend. Females lack the long, sword-like piercer, but are otherwise indistinguishable from *Spathidexia*.

341. Aristomeres 1 and 2 elongate (Fig. 135). Apical scutellar hairs crossed. Abdomen reddish. Ovipositor reduced to concentric sclerites, not protrusible .... ***Impeccantia*** Reinhard
1 sp., *claterna* Reinhard; southwestern U.S.A.

Aristomeres 1 and 2 minute. Apical scutellar setae divergent. Abdomen of female gray or brown pruinescent, slender and somewhat laterally compressed. Ovipositor long slender telescopic, normally fully concealed within abdomen (Fig. 259) .... ***Dolichotarsus*** Brooks, in part
see couplet 149

342. Arista lateromedially flattened, knife-like; aristomere 3 dilated at one-third distance from base (Fig. 136). Ocellar bristles lateroclinate (as in Figs. 21, 108). Scutellum with two or more straight preapical bristles arising anterodorsal to apical scutellar bristles and inclined at 45° (as in Fig. 187) .... ***Germaria*** Robineau-Desvoidy
1 undescribed sp.; Yukon

Arista cylindrical. Ocellar bristles proclinate. Scutellum without straight preapical bristles 343

343. First flagellomere with sharply pointed apex (Fig. 126). Scutellum short and broadly rounded, with crossed apical bristles and divergent lateral bristles arising rather far back between lateral and subapical position (as in Fig. 183) .... ***Acemya*** Robineau-Desvoidy[85]
5 spp.; widespread

First flagellomere rounded apically. Scutellum more triangular with truncate apex; subapical scutellar bristles long and divergent, arising from corners of truncate apex (as in Fig. 184) 344

344. Mid tibia without a ventral bristle. Abdomen of female arched ventrally, with telescopic ovipositor directed ventrally (as in Fig. 260) .... ***Trigonospila*** Pokorny, in part
see couplet 164

Mid tibia with well-developed ventral bristle. Abdomen of female not modified and ovipositor directed posteriorly 345

345. Frons with row of proclinate orbital setae extending anteroventrally to level of lowest frontal bristle (Fig. 52) .... ***Euhalidaya*** Walton, in part
see couplet 137

Frons with not more than two proclinate orbital bristles 346

346. Facial ridge thickened, protruding beyond parafacial, thus visible in profile, usually with small appressed setulae on lower half or more. Arista, when orange, thickened nearly to apex (Fig. 128) .... ***Phasmophaga*** Townsend, in part
see couplet 139

Facial ridge narrow, without setae. Arista thickened only at base, tapering to long slender apex (as in Fig. 134) 347

347. Katepisternum with two bristles .... ***Anisia*** Wulp, in part
see couplet 158

Katepisternum with three bristles .... ***Opsomeigenia*** Townsend, in part
see couplet 161

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[85] Also included are all species formerly placed in *Hemithrixion* Brauer & Bergenstamm, which differ only in lacking vein M beyond the bend.

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HIPPOBOSCIDAE 111

T. C. MAA AND B. V. PETERSON

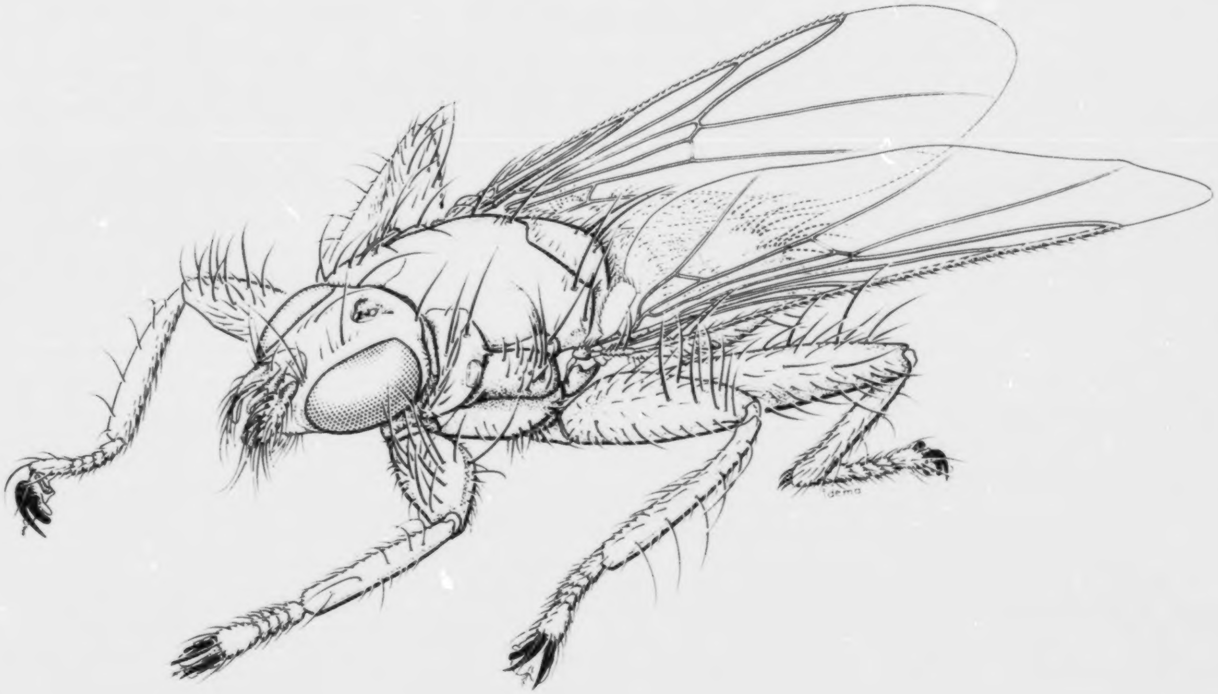


Fig. 111.1. Female of *Ornithomya anchineuria* Speiser.

Robust more or less dorsoventrally flattened flies (Fig. 1), 1.5–12.0 mm long, usually dull with variable and poorly defined pale markings, and richly setose. Antenna and mouthparts highly specialized. Wing usually fully developed, rarely reduced or absent. Abdomen, particularly in female, mainly membranous. Aedeagus and gonopods of male simple, retracted into abdomen when at rest. Larva completing development in uterus of female.

Adult. Head: prognathous, rather broad and moderately flattened (Figs. 2–7), with mouthparts displaced anteriorly so head is somewhat triangular in profile (Figs. 8, 9), and with its upper surface horizontal or descending forward; bristling light to moderate. Eyes separated in both sexes; eye large, usually horizontally elongate, rarely reduced, bare; ocelli often well-developed but sometimes vestigial or absent. Vertex (called postvertex by most previous authors) well-developed, bearing ocellar triangle; inner vertical bristles long; outer vertical bristles absent; orbital bristles few to numerous. Frons (called mediovertex by most previous authors) large and well-developed, almost always with a soft wrinkled membranous median frontal vitta, sometimes bearing interfrontal setae or bristles, and with lateral sclerotized fronto-orbital plates that sometimes bear fronto-orbital setae or bristles; ptilinal fissure conspicuous; lunule usually large and conspicuous, shiny and bare, with a variably distinct suture separating it from face or sometimes fusing anteriorly, often imperceptibly, with facial sclerite. Face variable in size, sometimes produced at each anterolateral corner, and sometimes uniting with parafacial to surround and isolate antennal socket; face bare, but ridge enclosing anteroventral margin of antennal socket often bristled. Clypeus greatly reduced, membranous to lightly sclerotized. Antenna highly modified, immovable or with movement greatly restricted, lying in a deep single antennal socket or in paired sockets; scape usually small but usually recognizable, sometimes completely separated from lunule by a distinct suture and bearing stout setae, or more or less fused with lunule but recognizable by presence of one or more stout setae, or completely fused with lunule without external indication of its presence; pedicel constituting the largest of the antennal segments and enclosing the first flagellomere, rounded in shape, and with or without an antennal appendage; this appendage dorsally flattened, leaf-like, bearing numerous setae and bristles; dorsolateral longitudinal suture on pedicel usually distinct; arista protruding from pedicel, spatulate, bipectinate, or variously branching. Palpus one-segmented, nearly always well-developed, rarely reduced or vestigial, compressed laterally but with concave inner surface serving as sheath for labium, and usually heavily bristled; labium bulbous basally, with the remainder needle-like, and terminating in tiny labella with a double crown of prestomal teeth; labium retractable when not in use and concealed in subcranial cavity and by palpi.

Thorax: flattened, about one-third or less as high as width of scutum (Fig. 1); lateral surface vertically flattened or concave, with dorsal margin variably folded dorsomedially so that part of upper lateral surface is dorsal in position; ventral surface or katepisternum broadened and flattened, widely separating each pair of coxae (Fig. 35). Antepronotum reduced, more or less concealed; postpronotal lobes variably developed but sometimes with anterolateral angle strongly produced lobe-like on each side of base of head, and sometimes enclosing anterior spiracle; this spiracle usually conspicuous and more or less dorsally situated (Figs. 1, 33). Scutum large, divided behind midlength into a larger presutural area (prescutum of authors) and a smaller postsutural area (scutum of authors) by a transverse suture; transverse suture sometimes complete, or variably incomplete to faintly indicated laterally; median scutal suture also present, variably distinct and variably complete, sometimes meeting or even continuing posteriorly beyond transverse suture to near scutellum; in *Melophagus ovinus* (Linnaeus) a continuation of this median scutal suture apparent, seeming to extend to hind margin of scutellum; bristling highly variable, with postpronotal, notopleural, supra-alar, postalar, pre- and post-sutural dorsocentral, and pre- and post-sutural acrostichal bristles appearing in various combinations and numbers, or sometimes absent. Scutellum (Figs. 18, 19, 21, 22, 24) usually large and well-developed, although sometimes small, varying from subtriangular to rectangular with parallel anterior and posterior margins; apical and discal bristles and setae few to numerous, rarely absent. Laterotergite of postnotum either gently or strongly raised as a convex process, and in turn sometimes bearing a digitiform process.

Wing fully developed (Figs. 10–14, 16, 17), but sometimes falling off soon after emergence, reduced (Fig. 15), or very rarely represented by a solid subcylindrical knob (Fig. 33); membrane of wing often with microtrichia in varying patterns having some taxonomic importance. Veins usually crowded toward anterior margin; distal part of posterior veins sometimes weak and not reaching wing margin; venation simple and nearly complete as in *Ornithomya* Latreille (Fig. 14), or variously reduced as in *Myophthiria* Rondani (Fig. 15), *Neolipoptena* Bequaert (Fig. 10), and *Lipoptena* Nitzsch; crossvein bm-cu absent or very faintly indicated; crossvein in *Neolipoptena* and *Lipoptena* long, probably consisting of elements of r-m, M, CuA$_1$, and possibly dm-cu; in many genera otherwise having a nearly complete venation, either CuA$_1$ or A$_1$ + CuA$_2$ strongly reduced and hardly discernible (Fig. 13). Alula, calypter, and halter present, rarely reduced or absent.

Legs robust, moderately short, often strongly bristled; coxae short but greatly swollen, femora variously swollen, tibiae less swollen to somewhat flattened, and hind tibia sometimes with a slight swelling or depression in basal half. Tarsomeres short; first tarsomere sometimes more elongate than next three tarsomeres combined; apical tarsomere the largest. Tibiae and tarsi often with a longitudinal series of sensory pores and setae. Claws stout, simple (Fig. 25) or bifid, and with a prominent flattened heel-like base (Fig. 26); empodia hairy or feathery; pulvilli paired and pad-like, often soft and elongate; claws, pulvilli, and apical lobes of certain tarsomeres of same leg sometimes aymmetric.

Abdomen: extensively membranous, particularly in female (Fig. 33), with seven pairs of spiracles in both sexes; tergite 1 often represented by a pair of variably developed lateral plates in which or in front of which are located anterior spiracles on each side; these plates either free, or partly or entirely fused with tergite 2, thus forming syntergite 1 + 2; tergite 2 large, sometimes free but usually fused with tergite 1, sometimes with margins projecting somewhat ventrally and more often posteriorly as short to moderately long blunt or pointed processes; one or more paired or unpaired tergites sometimes following syntergite 1 + 2, identifiable by position of spiracles; tergite 6 and tergite 7 most frequently consisting of plates, but these vary considerably in degree of development; tergite 8 membranous in female. Sternite 1 rarely absent, usually represented by a heavily sclerotized plate with hind margin either transverse, convex, or concave, and sometimes with posterolateral margins projecting arm-like posteriorly; remaining ventral surface of abdomen membranous, often densely setose or bristled, sometimes with narrow bare strips denoting segmental limits; female sometimes with sternites 6 and 7 present as small variously sclerotized plates bearing one to several setae or bristles, with sternite 6 usually smaller and weaker than sternite 7; male sometimes with a pair of small or large sclerotized plates representing sternite 5, but sternites 6 and 7 membranous.

Terminalia of female (Fig. 27) simple, but variable. Sometimes a tiny dorsomedial sclerite, probably representing the epiproct, present just anterior to and closely associated with cerci. Cerci (anal frame of previous authors) sometimes present as small to moderately large flap-like setose structures or as slender setose ring-like structures, and sometimes separated dorsomedially by a tiny epiproct or fused dorsomedially; cerci not fused ventrally, but closely associated with hypoproct so that they appear to be fused. Sternite 8 (anterior genital plate or ventral genital plate of previous authors) often absent, but sometimes present as a U-shaped or subtriangular-shaped or transverse bar-like sclerite just anterior to genital opening. Hypoproct (posterior genital plates or genital plate of previous authors) small to large, simple to complex, membranous or sclerotized, and sometimes at least partly retractable internally; hypoproct usually consisting of a single structure, but in more complex forms seemingly composed of two or three united pieces with or without pale lines of apparent demarcation, and often with one or two variably developed raised ridges or rims; although hypoproct situated posterior and dorsal to genital opening, its seemingly multistructural nature with its sclerotized rims or ridges suggests it might contain fused remnants of sternite 10. Two or three spermathecae (so-called forward glands) present, possibly functioning in the storage of spermatozoa.

Terminalia of male simple (Figs. 29, 30, 33, 34), retracted into abdomen when at rest and exserted for mating, and according to Zaka-ur-Rab (1979), most likely rotated through 360°. Syntergosternite 7 + 8 (genital synsegment of Zaka-ur-Rab 1979) variably developed from a slender weakly sclerotized half-ring-like sclerite to a broader saddle-like sclerite that may be variably excavated or emarginate dorsomedially along either anterior or posterior margin or both; composite nature of this syntergosternite often distinctly evident. Epandrium (anal frame of authors) a narrow ring-like setose sclerite that may be continuous or narrowly separated dorsomedially into two halves, with ventral margin of each side often widening; surstyli sometimes present, in form of small setose lateroventral plates or larger lobes or flaps articulating with ventral margins of epandrium (Zaka-ur-Rab 1979); these processes sometimes called genital styles (Cole 1927), gonocoxites (Bequaert 1953), lateral processes or plates or Seitenfortsätze (Theodor 1963, Theodor and Oldroyd 1964), and praegonites (Schlein and Theodor 1971, Theodor 1975). Cerci fused, apparent externally as a flattened sclerotized rod-like or plate-like sclerite; this sclerite setose distally, continuing anteriorly into genital pouch, and situated ventromedial to and articulating with epandrium; this structure previously known as anal sclerite (Theodor 1963, Theodor and Oldroyd 1964), rudimentary surstyli (Schlein and Theodor 1971), and posterior part of sternite 9 (Schlein and Theodor 1971, Theodor 1975); cerci sometimes greatly reduced and sometimes very lightly sclerotized or membranous, and sometimes apparently absent. Sternite 10 sometimes present in form of a short rod extending ventrally from anterior (internal) base of cerci to dorsal margin of base of aedeagus and gonopods. Hypandrium a relatively large trough-like heavily sclerotized plate fused with gonopods; gonopods elongate, subtriangular to digitiform, tubular, extending posteriorly on each side of aedeagus and exserted at same time as aedeagus during copulation, and usually beset with several microsetae and tubular sense organs; gonopods referred to previously as parameres (Theodor 1963, Theodor and Oldroyd 1964), postgonites (Schlein and Theodor 1971, Theodor 1975), interior forceps (Cole 1927), claspers (Roberts 1927), penis valves (Bequaert 1953), and claspettes (Zaka-ur-Rab 1979); true parameres apparently absent or fused with gonopods, but in some cases, remnants of parameres possibly represented by two short slender rod-like structures that extend distally from dorsal base of aedeagus and fuse with anterodorsal base of gonopods; aedeagus rather large, sometimes rod-like and slender, or broader and cone-shaped with sclerotized dorsal rods and sometimes sclerotized laterally; aedeagal membrane usually with fine setae or spinules and sometimes with stouter spines; aedeagal apodeme well-developed, flattened and plate-like, articulating with hypandrium; hypandrium and aedeagal apodeme enlarging and extending anteriorly with age of adult; aedeagal apodeme somewhat rod-like in newly emerged males but becoming sometimes more flattened and triangular in outline in old males.

Egg. Elongate cylindrical, tapering anteriorly, blunter posteriorly, very slightly concave dorsally. Micropylar pores lying in funnel-shaped depression at anterior end. Few known.

Larva. Three larval instars developed. First instar maggot-like, with faint traces of segmentation, and with eight pairs (two thoracic, six abdominal) of rudimentary lateral spiracles; a nipple-like projection bearing mouth and a pair of minute papillae present anteriorly; anus and a pair of spiracles evident posteriorly, lying together on a spiracular plate; cephalopharyngeal skeleton and mandibles absent. Second instar similar to first, but with a plumper ellipsoidal shape. Third instar barrel-like; a transverse circular seam and a longitudinal semicircular seam (along which the adult breaks open and emerges from puparium) evident anteriorly, as well as functionless apertures of thoracic spiracles; a pair of plates or lobes present posteriorly, each bearing three spiracles (in *Melophagus* Latreille) or three curved series of spiracular pores (in all other genera whose larvae are known), in addition to an anus; lateral abdominal spiracles completely lost.

Puparium. Similar to third-instar larva, but with cuticle much more hardened and darkened. Circular and semicircular seams slightly more significant; polypneustic lobes at posterior end more protruding.

Biology and behavior. Adults of all species are ectoparasitic, feeding on the blood of birds and mammals. Some species are host specific whereas others feed on an array of hosts that seems to be determined as much by ecological factors as by physiological factors or by their phylogenetic relationships. Birds are the most frequent hosts but some ungulates and a few other mammals also serve as hosts for a few species. Because some species attack domestic animals, especially sheep, they can be of considerable economic importance. Instances of about 13 species biting humans have been recorded, but such occurrences are accidental and relatively rare. Most species are fully winged and are fairly good flyers, but a few have aberrant wings and others lose part (*Allobosca* Speiser) or nearly all (*Lipoptena* and *Neolipoptena*) of their wings after settling on their host for one or more days (Haarløv 1964); *Melophagus ovinus* has rudimentary wings and no halteres. Consequently, some species can leave their host whereas others must remain on the host for the duration of their life cycle. The female reaches sexual maturity usually a few days after emergence. Some species mate only once in their lifetime, whereas *Melophagus* can mate repeatedly. Spermatozoa and other male secretions from these multiple matings may possibly help to nourish developing larvae (Berlese 1899 as quoted by Bequaert 1953, p. 92; Corbet 1956). The egg and larva develop in the female uterus, where secretions from the milk glands nourish the larva until its maturity. Only one mature ovum is produced at a time, which consequently develops into a single larva in the female. When fully grown, the larva is usually extruded away from the host and falls to the surrounding substrate, where it rapidly changes into a puparium. Occasionally fully formed puparia are found on the host, but these presumably eventually fall to the ground. Usually one generation occurs each year. A single female can produce up to seven or eight or more mature larvae during her lifetime. Phoresy between biting lice and hippoboscid flies is well known (Keirans 1975). Phoresy between hippoboscids and Psocoptera, Thysanoptera, and pseudoscorpions has also been reported but such cases are probably rare and accidental.

Many informative studies on the biology of hippoboscid flies have been published. Some of the more recent papers are those by Bequaert (1953), Corbet (1956, 1961), Bennett (1961), Hill (1962, 1963), Couch (1963), Klei and DeGiusti (1975*a*, *b*), and Hafez *et al.* (1977). Askew (1971) presented a good summary of hippoboscid biology. Many papers have been published on ked fly biology, their economic importance, and control, of which the following are noteworthy: Swingle (1913), Cowen (1943), Macleod (1948), Evans (1950), Kemper and Peterson (1953), Pfadt *et al.* (1953), Nelson and Slen (1953), Whiting *et al.* (1954), Nelson *et al.* (1957), Nelson and Qually (1958), and Nelson (1962).

Classification and distribution. About 19 genera and 150 species are known in the world fauna, of which 13 genera containing 31 species and two subspecies have been reported from the Nearctic region. The North American species have been monographed and cataloged by Bequaert (1942, 1954–1957, 1965). Recently, Griffiths (1972) lumped the families Nycteribiidae and Streblidae with the Hippoboscidae, but his classification is not followed here. Three subfamilies are currently accepted. The subfamilial name Lipopteninae Speiser has priority over Melophaginae Bezzi; the subfamily Hippoboscinae Samouelle is represented in North America solely by *Hippobosca longipennis* Fabricius, a species introduced with zoo animals that served as its host; Ornithomyinae Bigot, as now recognized, includes the four other subfamilies that Bequaert (1954, 1965) recognized previously. The tribes and subgenera used by Bequaert are not included in the key presented here. The generic names *Ornithomya* and *Myophthiria* are accepted here in their original rather than emended spellings (i.e. *Ornithomyia* and *Myiophthiria*); and *Lynchia* Weyenbergh is replaced with *Icosta* Speiser following a reinterpretation of the original description (Maa 1969). Three species, *Pseudolynchia canariensis* (Macquart), *Lipoptena cervi* (Linnaeus), and *Melophagus ovinus*, are immigrants from the Palaearctic region; a fourth species, *Icosta ardeae* (Macquart), occurs in both the Old and the New worlds, but different subspecies of it are usually recognized in Eurasia and North America. Two species, *Icosta hirsuta* (Ferris) and *Lipoptena depressa* (Say), are endemic to North America.

The family is cosmopolitan but is more richly represented in the tropics and subtropics than elsewhere. According to Bequaert (1950) the 50th parallel represents the northern limit for the family in the New World. Most of the species collected further north than this probably represent accidental summer occurrences. Bequaert (1950) recorded Takotna, Alaska (63°N, 165°W), as the northernmost distribution record for the family in the New World.

The only known fossil of the family, *Ornithomya rottensis* (Statz), is from Upper Oligocene formations in Germany (Maa 1966).

Key to genera

1. Ventral surface of thorax usually with only scattered soft setae and stiff bristles, but when densely and evenly setose (*Ornithoica* Rondani), then most setae fine and soft and only a few are spiniform. Basal abdominal sternite distinctly smaller than scutellum, its hind margin transverse to convex. Wing not caducous, and when fully developed, CuA_1 and $A_1 + CuA_2$, or both, often prominent (Figs. 14, 17). Normally parasitic on birds (and in the Old World also on certain mammals other than artiodactyls) 2

Ventral surface of thorax with fairly dense setae that are rather evenly spaced and almost entirely spiniform. Basal abdominal sternite distinctly larger than scutellum, its posterior margin strongly concave or rarely convex, e.g. *Neolipoptena ferrisi* (Bequaert). Wing, when fully developed and attached, with CuA_1 and A_1 indicated as faint colorless lines (Fig. 10). Normally parasitic on artiodactylous mammals .... LIPOPTENINAE 11

2. Antepronotum clearly visible in dorsal view; postpronotum rounded, not produced anteriorly as conical lobes. Wing membrane of all open cells distinctly wrinkled (Fig. 17) .... HIPPOBOSCINAE .... ***Hippobosca*** Linnaeus

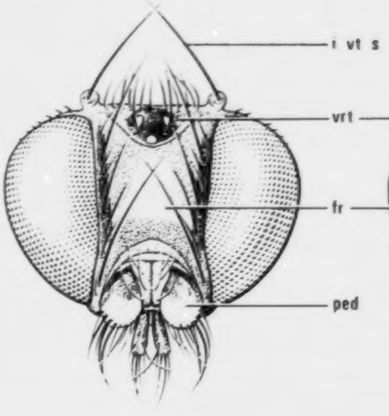
1 sp., *longipennis* Fabricius; introduced by zoo animals serving as hosts

Antepronotum not or only scarcely visible in dorsal view; postpronotum conspicuously produced into a pair of conical lobes on either side of head. Wing membrane of open cells not wrinkled (Fig. 11) .... ORNITHOMYINAE 3

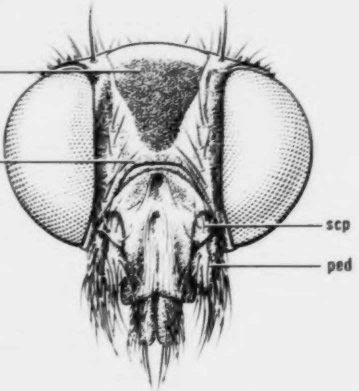
3. Inner vertical bristle arising from nipple-like tubercle (Fig. 2). Hind margin of wing ciliate throughout; R_{4+5} at its section distal to level of apex of R_{2+3} running almost contingent with C (Fig. 11). Tarsal claws simple but seemingly bifid (Fig. 25) ..... ***Ornithoica*** Rondani

2 spp.; widespread in U.S.A. and southern Canada; Bequaert 1954, Maa 1966

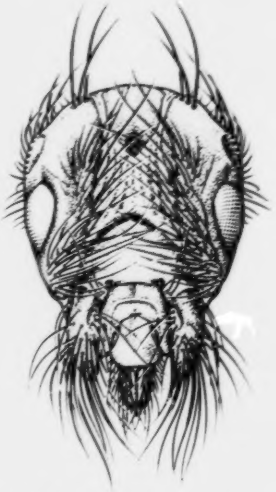
Inner vertical bristle normal, not arising from nipple-like tubercle (Figs. 3–7). Hind margin of wing at most with few cilia near base; R_{4+5} normal, well-separated from C except at extreme apex (Figs. 12–14, 16). Tarsal claws bifid but seemingly trifid (Fig. 26) 4



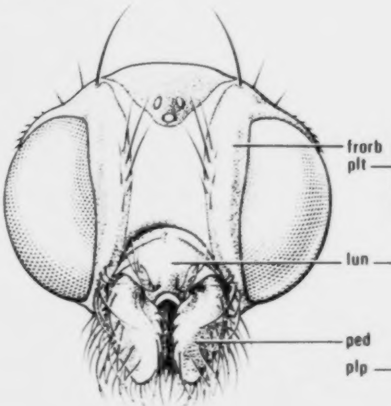
2 Ornithoica vicina ♀



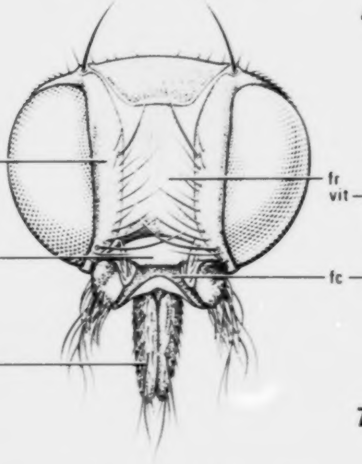
3 Olfersia fumipennis ♂



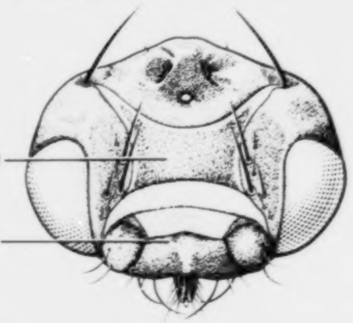
4 Myophthiria fimbriata ♂



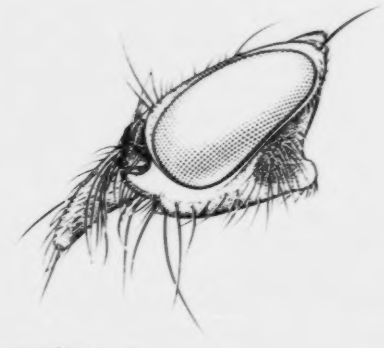
5 Ornithoctona erythrocephala ♀



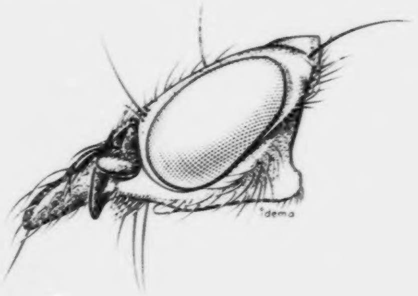
6 Icosta americana ♂



7 Lipoptena depressa pacifica ♀



8 Icosta americana ♂



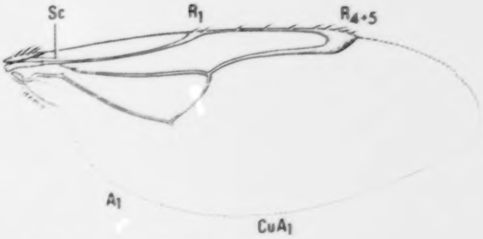
9 Microlynchia pusilla ♀

Figs. 111.2–9. Heads: (2) *Ornithoica vicina* (Walker); (3) *Olfersia fumipennis* (Sahlberg); (4) *Myophthiria fimbriata* (Waterhouse); (5) *Ornithoctona erythrocephala* (Leach); (6) *Icosta americana* (Leach); (7) *Lipoptena depressa pacifica* Maa; (8) *Icosta americana*; (9) *Microlynchia pusilla* (Speiser).

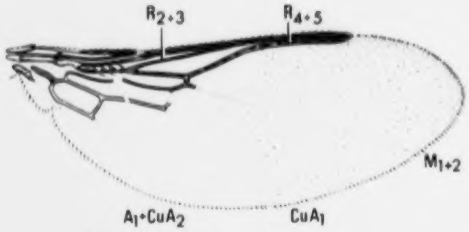
Abbreviations: fc, face; fr, frons; frorb plt, fronto-orbital plate; fr vit, frontal vitta; i vt s, inner vertical bristle; lun, lunule; ped, pedicel; plp, palpus; scp, scape; vrt, vertex.

4. Wing when fully developed with both CuA_2 and $A_1 + CuA_2$ well-developed; when wing greatly reduced (about one-half as long as thorax) (Fig. 15), then eye much narrower than fronto-orbital plate (Fig. 4). Abdomen with dorsomedian area not transversely striolate. Antenna distinctly longer than palpus; apex acute or narrowly rounded, extending well beyond antennal pit 5

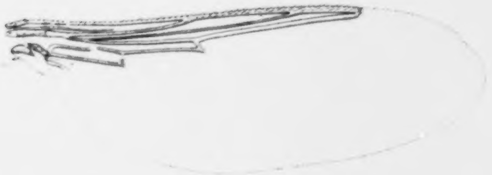
Wing always well-developed, always lacking complete CuA_2; A_1 weakly visible except at extreme base (Figs. 12, 13). Eye always much broader than fronto-orbital plate (Figs. 3–6). Abdomen dorsomedially with a broad transversely striolate area. Antenna distinctly shorter than palpus; apex broadly rounded, not or just slightly extending beyond antennal pit 8



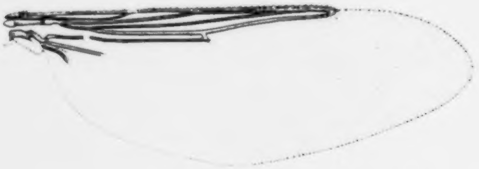
10 Neolipoptena ferrisi ♀



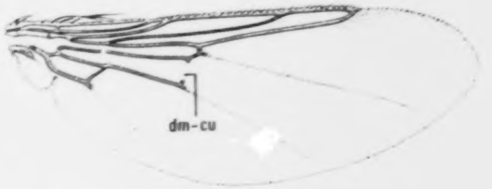
11 Ornithoica vicina ♀



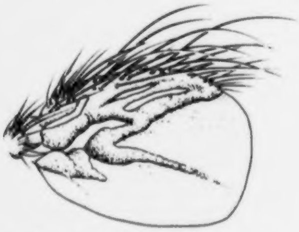
12 Icosta americana ♀



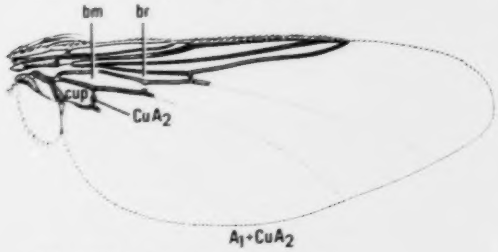
13 Pseudolynchia canariensis ♀



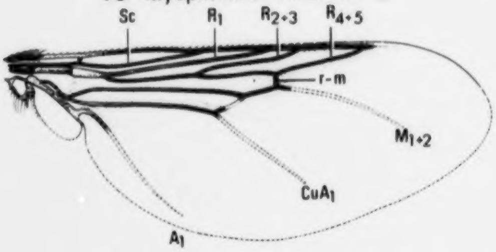
14 Ornithomya anchineuria ♀



15 Myophthiria fimbriata ♂



16 Stilbometopa impressa ♀



17 Hippobosca longipennis ♀

Figs. 111.10–17. Wings: (10) *Neolipoptena ferrisi* (Bequaert); (11) *Ornithoica vicina* (Walker); (12) *Icosta americana* (Leach); (13) *Pseudolynchia canariensis* (Macquart); (14) *Ornithomya anchineuria* Speiser; (15) *Myophthiria fimbriata* (Waterhouse); (16) *Stilbometopa impressa* (Bigot); (17) *Hippobosca longipennis* Fabricius.

5. Antennal appendage (dorsal process of pedicel) relatively small; those of both antennae separated by a distance as wide as, or more often much wider than, width of an appendage; its dorsal surface convex and extensively setose (Figs. 1, 4). Abdomen of male lacking paired pregenital sternal plates. Wing often fully developed (Fig. 14), rarely greatly reduced (*Myophthiria*) (Fig. 15) 6

Antennal appendage large and broad; those of both antennae lying close to one another by a distance not wider than an appendage; its dorsal surface fairly flat and lightly setose (Fig. 5). Abdomen of male with a pair of large pregenital sternal plates. Wing always fully developed (Fig. 16) 7

6. Wing fully developed, about three times as long as thorax; venation normal, with six longitudinal veins behind Sc and with three crossveins (Fig. 14). Abdomen in both sexes (of Nearctic species) with three well-defined unpaired median tergal plates. Eye distinctly broader than fronto-orbital plate (Fig. 1) .... ***Ornithomya*** Latreille

2 spp.; widespread from Alaska southeast to Saint Pierre and Miquelon, and U.S.A.; Maa 1969

Wing greatly reduced, only about one-half as long as thorax; venation much reduced (Fig. 15). Abdomen in both sexes (of Nearctic species) with no well-defined unpaired median tergal plates. Eye distinctly narrower than fronto-orbital plate (Fig. 4).... ***Myophthiria*** Rondani

1 sp., *fimbriata* (Waterhouse); U.S.A. west from Nebraska to Arizona and north to Utah and Wyoming

7. Laterotergite strongly produced into an anvil-shaped process (Fig. 19); metabasisternum[1] posterolaterally produced into an acute process overlapping base of hind coxa (Fig. 20); strong scutellar bristles 40–50 in number, arranged comb-like (Fig. 19). Ocelli absent .... ***Stilbometopa*** Coquillett

3 spp.; widespread in southern half of U.S.A.; Bequaert 1955

Laterotergite only weakly raised, without a process (Fig. 18); metabasisternal process absent; strong scutellar bristles fewer than 12 in number, not arranged comb-like (Fig. 18). Ocelli well-developed (Fig. 5) .... ***Ornithoctona*** Speiser

2 spp.; widespread in U.S.A. and southern Canada; Bequaert 1954

8. Frontal vitta either apparently confluent with vertex or, when weakly definable, then much smaller and shorter than vertex; anterolateral processes of face subparallel, markedly shorter than face proper (Fig. 3). Scutellum lacking preapical bristles; laterotergite always strongly produced into a somewhat reverted L-shaped bar at side of scutellum (Fig. 21) .... ***Olfersia*** Leach

4 spp.; widespread in U.S.A. and southern Canada; Bequaert 1957

Frontal vitta usually well-defined, much longer than vertex; anterolateral processes of face strongly divergent, markedly longer than face proper (Fig. 5). Scutellum with a pair of strong preapical bristles; laterotergite either weakly raised (Fig. 24) or strongly produced into a conical process (Fig. 22) 9

9. Wing with crossveins r-m and dm-cu present; crossvein dm-cu with a transparent whitish spot anteriorly but fully pigmented and sclerotized posteriorly (Fig. 12). Vibrissal angle of head, in profile, broadly rounded (Fig. 8), or subangulate but never strongly protruding .... ***Icosta*** Speiser

8 spp.; widespread in U.S.A. and southern Canada; Maa 1969

Wing with only crossvein r-m present (Fig. 13). Vibrissal angle of head, in profile, strongly produced into a sharp angulate process (Fig. 9) 10

10. Hind margin of scutellum straight or nearly so, sharply edged, with a transverse series of setigerous tubercles near each end (Fig. 24); laterotergite weakly convex (Fig. 24); metabasisternum posterolaterally produced into a spur-like process overlapping base of hind coxa (Fig. 23) .... ***Pseudolynchia*** Bequaert

2 spp.; British Columbia and U.S.A.; Bequaert 1955, Maa 1966

Hind margin of scutellum distinctly convex and curved, edge rounded, lacking setigerous tubercles (Fig. 22); laterotergite strongly produced as a conical process (Fig. 22); metabasisternum posterolaterally truncate .... ***Microlynchia*** Lutz, Neiva, & Lima

1 sp., *pusilla* (Speiser); widespread in U.S.A.

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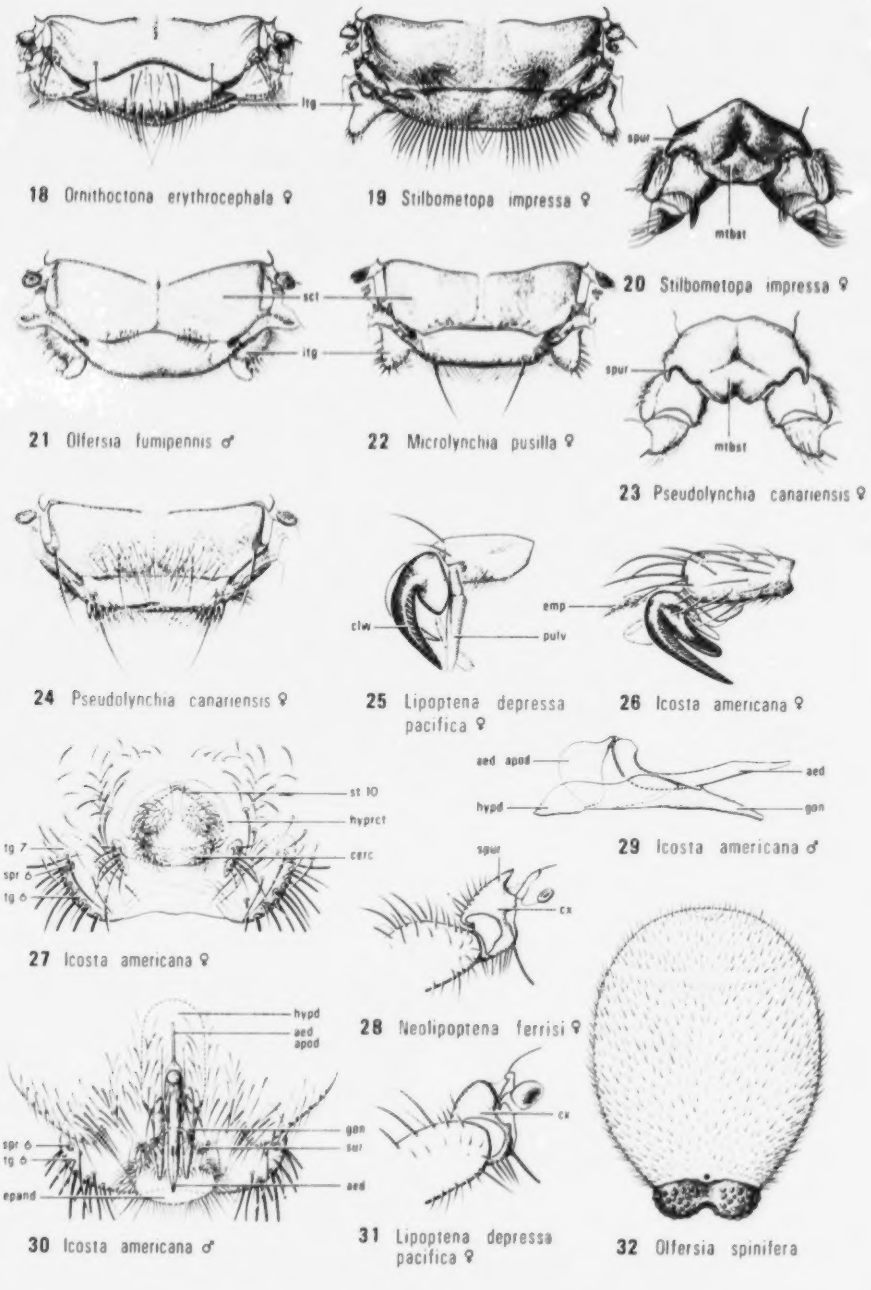
[1] The term metabasisternum is retained here following previous usage, e.g. Crampton (1942), Schlein (1970), and others. However, the true composition of this structure remains in question because some pleural elements are possibly included in its formation.



18 Ornithoctona erythrocephala ♀

19 Stilbometopa impressa ♀

20 Stilbometopa impressa ♀

21 Olfersia fumipennis ♂

22 Microlynchia pusilla ♀

23 Pseudolynchia canariensis ♀

24 Pseudolynchia canariensis ♀

25 Lipoptena depressa pacifica ♀

26 Icosta americana ♀

27 Icosta americana ♀

28 Neolipoptena ferrisi ♀

29 Icosta americana ♂

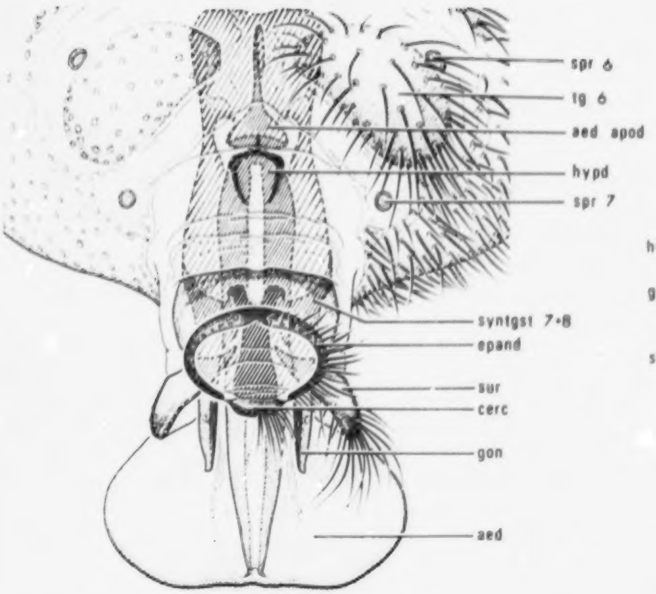
30 Icosta americana ♂

31 Lipoptena depressa pacifica ♀

32 Olfersia spinifera

Figs. 111.18–32. Thoracic structures, tarsal claws, coxae, male and female terminalia, and puparium: thoracic structures of (18) *Ornithoctona erythrocephala* (Leach), (19) *Stilbometopa impressa* (Bigot), (20) *Stilbometopa impressa*, (21) *Olfersia fumipennis* (Sahlberg), (22) *Microlynchia pusilla* (Speiser), (23, 24) *Pseudolynchia canariensis* (Macquart); tarsal claws of (25) *Lipoptena depressa pacifica* Maa and (26) *Icosta americana* (Leach); (27) female terminalia, in ventral view, of *Icosta americana*; (28) fore coxa of *Neolipoptena ferrisi* (Bequaert); (29) lateral view and (30) ventral view of male terminalia of *Icosta americana*; (31) fore coxa of *Lipoptena depressa pacifica*; (32) puparium of *Olfersia spinifera* (Leach).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; clw, claw; cx, coxa; emp, empodium; epand, epandrium; gon, gonopod; hypd, hypandrium; hyprct, hypoproct; ltg, laterotergite; mtbst, metabasisternum; pulv, pulvillus; sct, scutum; spr, spiracle; st, sternite; sur, surstylus; tg, tergite.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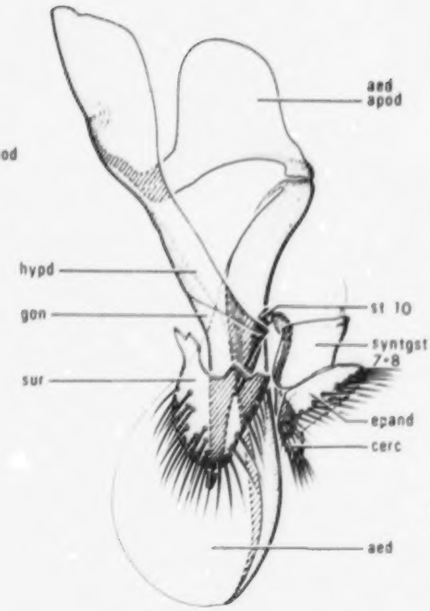
33 Hippobosca longipennis ♂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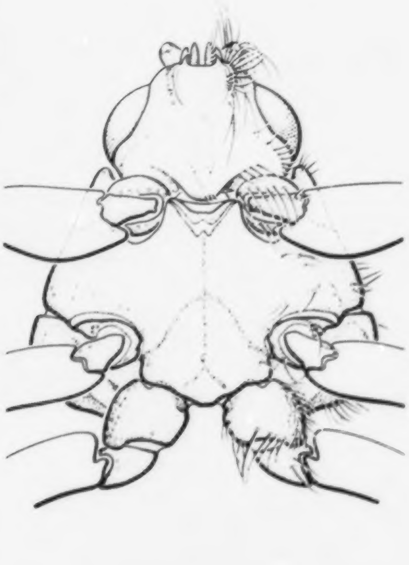
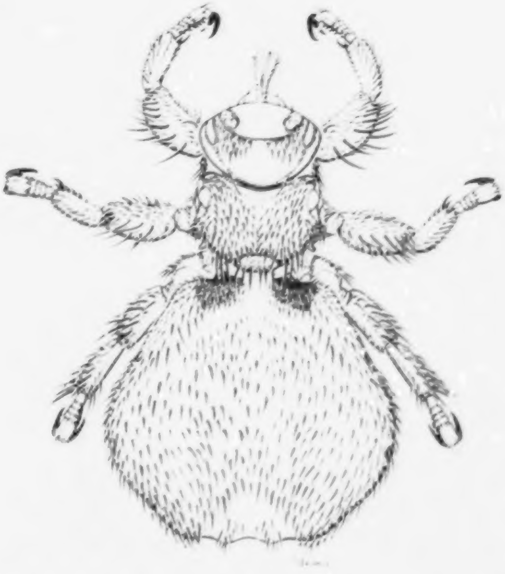
34 Hippobosca longipennis ♂



35 Ornithomya anchineuria ♀



36 Melophagus ovinus ♀

Figs. 111.33–36. Male terminalia, thorax, and habitus: (33) dorsal view and (34) lateral view of male terminalia of *Hippobosca longipennis* Fabricius; (35) head and thorax in ventral view of *Ornithomya anchineuria* Speiser; (36) female of *Melophagus ovinus* (Linnaeus).

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; gon, gonopod; hypd, hypandrium; spr, spiracle; st, sternite; sur, surstylus; syntgst, syntergosternite; tg, tergite.

11. Wing represented by a veinless solid subcylindrical knob; halter entirely absent. Eye about four times as long as wide, slightly narrower than antenna (Fig. 33) .... ***Melophagus*** Latreille

1 sp., *ovinus* (Linnaeus); introduced, widespread in U.S.A. and southern Canada

Wing either fully developed (Fig. 10) or, when dealated, represented by a veined transparent flat stump; halter present. Eye about as long as wide, about two times as wide as antenna (Fig. 7) 12

12. Fore coxa with a distinct retrograde spur posterodorsally (Fig. 28). Abdomen with no median tergites; sternite 1 elliptic, with convex hind margin. About 15 fronto-orbital bristles present on each side .... ***Neolipoptena*** Bequaert

1 sp., *ferrisi* (Bequaert); western Canada and U.S.A.

Fore coxa without a retrograde spur (Fig. 31). Abdomen with distinct median tergites; sternite 1 crescent-shaped, with a strongly concave hind margin. About two or three fronto-orbital bristles present on each side (Fig. 7).......................... ***Lipoptena*** Nitzsch

3 spp., 2 subspp.; Bristish Columbia and U.S.A.; Bequaert 1957; Maa 1965, 1969; Peterson and Maa 1970

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NYCTERIBIIDAE

112

B. V. PETERSON AND R. L. WENZEL

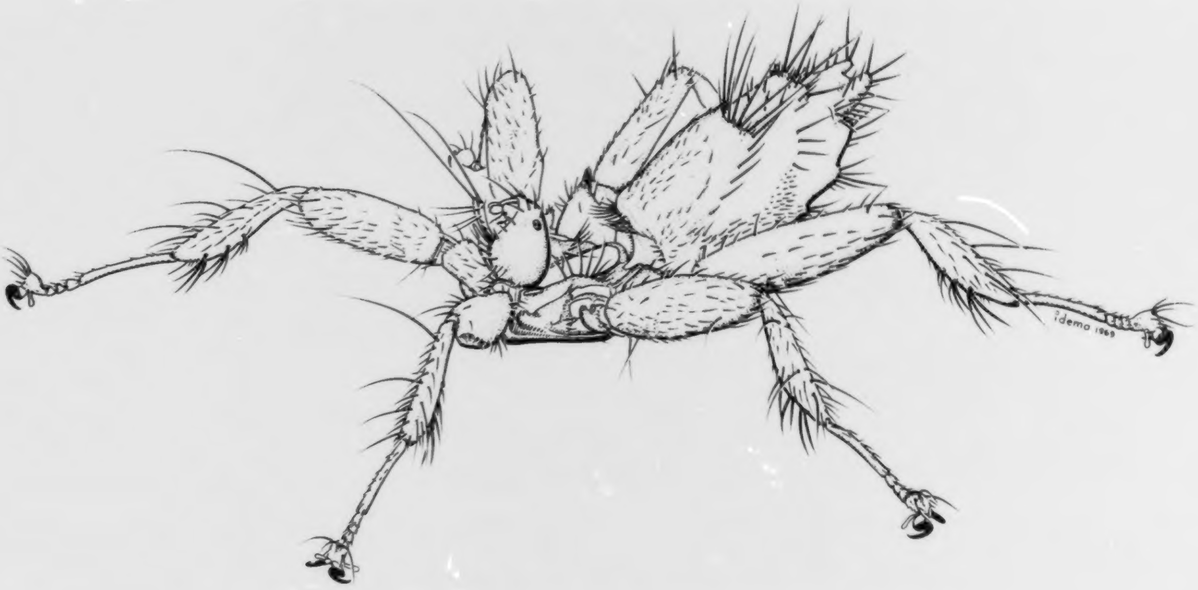
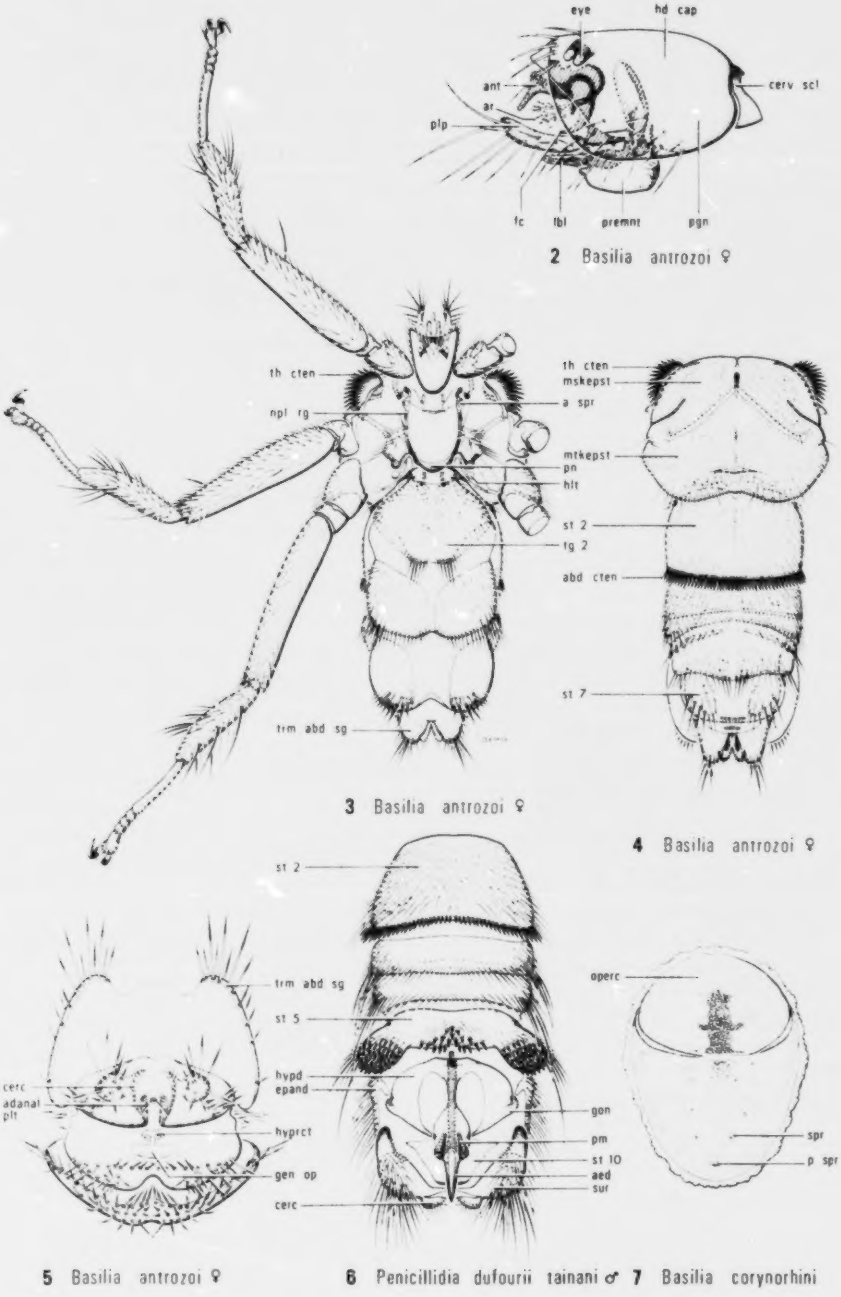


Fig. 112.1. Female of *Basilia forcipata* Ferris.

Small bristly spider-like flies (Fig. 1), ranging in length from about 1.5 to 5.0 mm, without scutellum and wings, but with halteres. Head folding back on thorax at rest, rotating forward and downward through about 180° for feeding. Thorax flattened dorsoventrally; ventral surface sclerotized; dorsal surface mainly membranous and supported by a reduced framework of sclerotized ridges and plates; most species with thoracic and abdominal ctenidia. Male with large clasper-like surstyli that fold anteriorly under apex of abdomen. Obligate blood-sucking ectoparasites on bats.

Adult. Head: situated middorsally near anterior margin of thorax but posterior to origin of front legs, at rest folding back so its dorsal surface, at least in part, lies in contact with scutum (Fig. 1), rotating forward and downward through about 180° for feeding; shape longer than wide, somewhat rounded, or compressed laterally or dorsoventrally; large helmet-like sclerite of head capsule (Fig. 2) mainly membranous anteriorly, variably membranous ventrally, and sclerotized dorsally with variable smaller membranous areas; sclerotized portion between membranous ptilinal area anterodorsally to thickened margin of occipital foramen posteroventrally probably consisting of fused elements of frons, vertex, and postcranium, anterolaterally continuous with genae below eyes, and posteriorly and lateroventrally continuous with postgenae; no sutures evident delimiting these areas of head capsule, but a variably developed median membranous strip present, separating postgenae ventrally. Frontal area usually with one or more pairs of short or long setae near anterior margin; vertex sometimes with a rather dense patch of nearly uniform setae on anterior half; gena with one or more rows of setae of variable length along anterior margin; postgena also sometimes with a few short or long setae ventrally. Eye sometimes absent, but when present, reduced, consisting of one or two, or rarely four, ocelli-like facets situated in a ring-like ocular sclerite; this sclerite sometimes reduced or absent. Ptilinum a flexible membranous strip that may be very narrow or wide enough to overlap bases of antennae dorsally, tapering ventrolaterally to gena on each side, sometimes with minute scale-like setae; this structure apparently not eversible nor used during emergence of adult from puparium. Face (fronto-clypeus of Jobling 1928) occupying most of anterior part of head, consisting of a movable sclerotized median facial plate; facial plate large and complex, e.g. *Cyclopodia* Kolenati, or reduced and simpler with ventral portion of facial area mostly membranous, or with a ventrolateral triangular or digitiform process on each side, e.g. *Penicillidia* (*Eremoctenia*) *vandueseni* (Maa); variably developed median facial carina and lateral antennal pits usually also present. Antenna moderately large in relation to size of head, appearing as a single compound segment, but consisting of two segments representing the pedi-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2 Basilia antrozoi ♀

3 Basilia antrozoi ♀

4 Basilia antrozoi ♀

5 Basilia antrozoi ♀

6 Penicillidia dufourii tainani ♂

7 Basilia corynorhini

Figs. 112.2–7. Head, thorax, abdomen, and puparium: (2) left lateral view of head of *Basilia antrozoi* (Townsend); (3) dorsal view of entire adult of *B. antrozoi;* (4) ventral view of thorax and abdomen of *B. antrozoi;* (5) posteroventral view of female terminalia of *B. antrozoi;* (6) ventral view of abdomen and male terminalia of *Penicillidia dufourii tainani* Karaman; (7) dorsal view of puparium of *Basilia corynorhini* (Ferris), redrawn from Ferris (1930).

Abbreviations: adb cten, abdominal ctenidium; adanal plt, adanal plate; aed, aedeagus; ant, antenna; ar, arista; a spr, anterior spiracle; cerc, cercus; cerv scl, cervical sclerite; epand, epandrium; fc, face; gen op, genital opening; gon, gonopod; hd cap, head capsule; hlt, halter; hypd, hypandrium; hyprct, hypoproct; lbl, labella; mskepst, mesokatepisternum; mtkepst, metakatepisternum; npl rg, notopleural ridge; operc, operculum; pgn, postgena; plp, palpus; pm, paramere; pn, postnotum; premnt, prementum; p spr, posterior spiracle; spr, spiracle; st, sternite; sur, surstylus; tg, tergite; th cten, thoracic ctenidium; trm abd sg, terminal abdominal segment.

cel and flagellum; scape apparently absent (Jobling 1928), or more likely, as suggested by Theodor (1975), fused with head capsule, or possibly fused with pedicel (Hennig 1941); pedicel (apparent first segment) largest, with a prominent dorsal prolongation and a smaller ventral prolongation; basal portion of pedicel swollen to surround flagellum (apparent second segment); a short dendriform arista present, projecting anteriorly below dorsal prolongation of pedicel; a longitudinal seam evident in pedicel of *Penicillidia dufourii tainani* Karaman (Hennig 1941). Proboscis short, consisting of a broad usually conical prementum (theca) and slender tube-like labella; apex of labella membranous and bearing minute spinules (prestomal teeth); palpus one-segmented, usually large, varying in shape from flattened and blade-like to slender and digitiform, to a combination of these types; marginal bristles usually present on outer surface of palpus, sometimes accompanied by additional bristles on outer surface; one or more of these terminal bristles usually very long. Jobling (1928) gave a detailed description of head and mouthparts.

Thorax: broad, compressed dorsoventrally, greatly modified; original limits of segments and their sclerites obscured; dorsal surface mainly membranous; ventral surface heavily sclerotized; cervical sclerites usually well-developed. Sclerotized U-shaped framework evident dorsally (Fig. 3), consisting of a longitudinal notopleural ridge extending posteriorly from near base of each anterior coxa to, and fusing with, postnotum, and fusing laterally with sclerotized pleural plates. Pronotum displaced posterodorsally, represented by a few (basically four) small sclerites around outside base of head; posteriormost of these forming two slender rod-like sclerites set at varying angles to each other, or these fused into a broader somewhat V-shaped or U-shaped sclerite; this sclerite usually connecting with anterolateral sclerite on each side, which in turn connect with longitudinal notopleural ridges of dorsal framework just in front of anterior spiracles; anterior spiracles enclosed by these ridges. Scutum represented by a membranous area enclosed by framework of notopleural ridges (notopleural sutures of authors) and postnotum; sclerotized pleural plates present lateral to each notopleural ridge and fused with it, probably composed of elements of notopleuron, anepisternum, and anepimeron; a lateral epimeral rod-like projection of this complex extending somewhat anteroventrally toward and articulating with anterodorsal aspect of mid coxa and posterodorsal corner of a somewhat triangular longitudinally oriented sclerite; this triangular sclerite situated dorsal to and running subparallel with anteroventral extension of mid coxa, and articulating through a much smaller sclerite bearing a crescent-like row of stout spines; movable thoracic ctenidium formed from these spines unique to Nycteribiidae but absent in a few genera, reportedly of coxal origin (Schlein 1970), but possibly also containing elements of anepisternum; notopleural ridge with a row or patch of notopleural setae, or with a single seta or none at all in some genera, and sometimes with a group of several minute setae near posterior end of usual row of notopleural setae; scutellum absent; postnotum variably rounded and variably raised like the hull of a boat, occasionally extending middorsally as a digitiform process. Metanotum reduced, with two short slender sclerotized rods extending a short distance into abdomen; metasternum internal, moderately sclerotized, and somewhat U-shaped; pleural sclerites of metathorax undifferentiated, fused into a single plate; however, an intersegmental suture present in some genera, running anteroventrally from metathoracic spiracle between mid and hind coxae, thus separating metathoracic pleural plate from mesothorax; posterior spiracle situated near base of halter. Wing absent. Halter short; pedicel slender; knob spherical to ovoid, usually pale in color, situated in a depression or groove of metathoracic pleural plate; this groove sometimes open or partly or completely closed by a sclerotized flap-like cover originating from median side of groove. Ventral surface of thorax (Fig. 4) flattened plate-like, composed of four (appearing as two) more or less fused sclerites representing each half of ventrally displaced katepisternal plates of mesothoracic and metathoracic segments; katepisternal plates divided by a longitudinal median sternal suture; mesothoracic plates divided from metathoracic plates by an inverted V-shaped (oblique) mesometasternal suture; this suture either fused and closed or membranous and open, but when closed, sometimes very faint and seemingly absent; anterior margin of mesokatepisternum broadly rounded to somewhat pointed and often notched medially, curving slightly upward to facilitate movement among hairs of host; katepisternal plates variously covered by mostly short setae; hind margin of metakatepisternal plate fringed with short or long setae, or with both.

Legs moderately long and stout, and rather densely setose with short and long to very long setae or bristles. Anterior and posterior coxae well-developed; anterior coxa rather long in some genera; middle coxa short, ring-like, composed of anteroventral triangular setose sclerite articulating anteriorly with a small sclerite that in turn articulates with posteroventral margin of thoracic ctenidium. Femora stout, with a pale ring of thinner integument near basal third or quarter; mid and hind femora sometimes with a few sensory pores anteriorly near base. Tibiae ranging from slender and cylindrical or spindle-shaped to broad, flattened, and blade-shaped, often about as long as femora, but sometimes considerably shorter; two or three rings of thinner integument sometimes evident; two to five rows of short or long setae sometimes present ventrally and usually present on distal half. Tarsal segments slender; first tarsomere usually longer than remaining tarsomeres combined, sometimes pseudoannulate with partial rings of thinner integument probably to allow flexibility; middle three tarsomeres very small; apical tarsomere stoutest, somewhat triangular, about as long as two or even three of preceding tarsomeres; claw simple, relatively large and stout; pulvilli pad-like; empodia absent.

Abdomen: tergites and sternites of both sexes usually bearing one or more rows of long or short setae, or both, along their posterior margins; discal setae also sometimes present in varying patterns and combinations; abdominal membrane (connexivum of authors) also with varying patterns and combinations of setae and spines, and some females of some genera (e.g. *Cyclopodia*) with various groups of long setae dorsally; arrangement and often numbers of setae and spines of taxonomic importance. Seven pairs of spiracles present in both sexes, but their positions vary considerably in females of different species.

Original number of tergites and sternites in female abdomen (Figs. 3, 4) obscured; seven tergites (tergites 1 and 2 fused) and seven sternites present only in the Neotropical genus *Hershkovitzia* Guimarães & d'Andretta; in some other genera two to four tergites sometimes present but these perhaps not reflecting the true segmentation of the abdomen; in some genera no tergites present between basal tergite and terminal segment (anal segment of authors). A small slender bare or setose sclerite present at base of abdomen on each side near anterior spiracle, called a postspiracular sclerite by most authors, but regarded here as a lateral remnant of sternite 1; this supposition supported by the presence of a short, but usually distinct, somewhat U-shaped, midventral, lightly to moderately sclerotized plate in all species examined, probably representing middle portion of sternite 1, and by the presence of very fine dorsal thread-like extensions of this plate that are directed toward anteroventral corners of syntergite 1 + 2; postspiracular sclerites present in all known genera except *Penicillidia* Kolenati, but this genus having a middle remnant of sternite 1 in all species examined. Sternite 2 (synsternite 1 + 2 of authors) largest of sternites, usually setose, sometimes with a median longitudinal suture; this suture sometimes only faintly indicated, sometimes absent; hind margin usually bearing a series of stout contiguous spines forming an abdominal ctenidium; ctenidium sometimes reduced or absent. Segments 3 and 4 usually membranous ventrally, their posterior margins often delimited by bare strips or rows of setae, occasionally with sclerotized sternites. Segments 5 and 6 sometimes membranous ventrally, but usually with sternites divided into lateral plates. Sternite 7 rarely absent, but when present, prominent to greatly reduced, or possibly fused with sternite 8, usually entire, rarely divided into lateral halves, and serving as a so-called ventral plate or ventral genital plate in the absence of sternite 8; ventral plate setose, with spines or spine-like setae on anterior or posterior margin. Sternites 8–10, if present, greatly reduced; one or more of these may be absent or not sclerotized and thus unapparent, or sometimes represented only by groups of tiny setae; sternite 9, if present, at least partially or wholly internal; sternite 10 (dorsal plate, dorsal genital plate) sometimes bearing setae or spinules, sometimes projecting lip-like, or absent; a small sclerite (anal sclerite of authors) midventral to cerci sometimes present, possibly representing the hypoproct or a remnant of sternite 10; two small but variable sclerites (adanal plates of authors) often present ventrolateral to cerci and sometimes fused with them, possibly representing dorsolateral remnants of hypoproct or sternite 10; this supposition supported by presence in some species of a thread-like extension projecting dorsally along anterior margin of cercus toward tergite 10. A pair of small tubular spermathecae present and functional.

Male abdomen (Fig. 6) with segmentation more distinctly preserved than that of female; six sclerotized tergites (tergites 1–6 or syntergite 1 + 2 plus four additional tergites) and five sclerotized sternites present before compound terminal segment. Sternites 1 and 2 as in female. Sternite 5 with hind margin broadly to narrowly convex, concave, or somewhat undulating; one or more comb-like rows of short stout spines usually present or sometimes a marginal series of long and short setae present either alone or in combination with stout spines; posterolateral lobes also sometimes present, bearing short spines. Epandrium (terminal segment, anal segment) consisting of a syntergosternite composed mainly of fused segments 7, 8, and 9; spiracle 7 often situated in anteroventral angle; sometimes a faint intersegmental suture present just ventral or posterior to this spiracle; epandrium often short, broad, and subtriangular or subrectangular, or sometimes long and slender; ventral margin sometimes somewhat sinuous, or with a small irregular sternite-like process, or with a small subtriangular plate at posterolateral angle that articulates with base of surstylus; a lateral process occasionally present on each side, bearing spines or setae. Tergite 10 represented by long, straight or variously curved and tapering surstyli (claspers, forceps, and cerci of authors); surstyli movable, folding anteriorly under epandrium, each articulating with corners of epandrium; each surstylus bearing various combinations of long and short setae, and sometimes with peg-like spinules. Cerci slender and somewhat ring-like, similar to those of female, bearing a marginal row of minute setulae; cercus closely associated with, and often fused with, base of surstylus, but usually with a faint suture delimiting area of fusion.

Sternite 6 sometimes membranous, or faintly sclerotized and sometimes greatly reduced, or possibly represented in some species by a slender sclerotized ridge posterior to and folding forward under hind margin of sternite 5 when at rest; in other species a slender sclerotized bar present representing this sternite, laterally becoming narrow and thread-like medially, or sometimes fused laterally with, but distinct from, sternite 7 or 7 + 8. Sternal elements of segments 7 and 8, when present, usually fused as a slender or sometimes moderately broad ventral band connected dorsally on each side with compound epandrium; posterior margin of this band sometimes straight or variously emarginate; these sternal areas sometimes delineated by a faint suture line, or rarely well-separated and present as two slender bands; a small irregular process sometimes present along ventrolateral margin of epandrium; a small isolated sclerite also sometimes present laterally, seeming to serve as a point of articulation for sternite 9; all these processes or small sclerites probably remnants of sternite 8. Sternite 9, the hypandrium (basal arc, subgenital plate of authors), well-developed, usually a U-shaped or Y-shaped or somewhat triangular sclerite, forming an anteroventral frame around base of genital complex; a well-developed hypandrial apodeme sometimes present; aedeagal guide also sometimes present in the form of an elongate somewhat digitiform or somewhat club-shaped or flattened plate occasionally fused with or articulated with posteromedial margin of hypandrium; gonopod when present reduced to small cap-like remnant dorsal to aedeagal guide and lateral to base of paramere; aedeagus usually consisting of two plate-like halves apically; these two portions sometimes fused trough-like ventrally and closed dorsally as well as sometimes ventrally by membrane, or sometimes entirely membranous with its walls strengthened by a slender rod-like sclerite; accessory membranous areas sometimes present, occasionally bearing short setulae or spinules; an eversible membranous structure (endophallus of Theodor 1967) also present in some species; aedeagal apodeme usually well-developed, sometimes absent; paramere usually well-developed and blade-like but reduced to a small subtriangular plate in some species, articulating basally with remnants of gonopod and sometimes apparently immovable, in most cases capable of being rotated laterally and posteriorly, usually bearing small setae and sometimes minute spinules. Sternite 10 (basal plate of authors) well-developed, plate-like, varying in shape and size.

Several studies have been published on various aspects of the morphology of adult Nycteribiidae. Some of the more useful general studies include those of Corradetti (1933), Guimarães (1946), Guimarães and d'Andretta (1956), Hennig (1941), Hiregaudar and Bal (1956), Massonnat (1909), Mukerji and Dasgupta (1954), Nowosad (1975), Speiser (1901), Theodor (1954, 1967, 1975), and Theodor and Moscona (1954). Other important studies include those of Jobling (1928) and Müggenburg (1892) on the head and mouthparts, Nussbaum (1960) and Schlein (1970) on the thorax, and Corradetti and Lupascu (1941*a*,*b*), Schlein and Theodor (1971), Theodor (1953), Verolini (1957), and Zaka-ur-Rab (1979) on genital structures. According to Cooper (1941), the $2n$ number of chromosomes for *Basilia myotis* Curran is 10.

Egg. Ovaries alternately giving rise to one ovum at a time. Solitary egg hatches after fertilization within female uterus, where the larva feeds, grows, and molts until mature (Leong and Marshall 1968, Marshall 1970).

Larva. Soft and white when laid, elliptic to ovoid, strongly convex dorsally, less convex ventrally but becoming flattened when pressed by female to substrate for adhesion to it, broader anteriorly, tapering posteriorly; abdomen with evidence of segmentation. A variable proboscis-like process evident immediately after deposition, highly mobile initially, bearing mouth opening; mouth opening capable of alternating from circular to slit-like or horizontally arcuate with a concavity pointing upward or downward; this proboscis-like process mostly withdrawn into anterior end of larva shortly after deposition; cephalopharyngeal skeleton and mandibles absent. Two pairs of abdominal spiracles present, connected by trachea; anterior spiracles broadly separated, apparently varying in position on abdomen according to species (Hennig 1952); posterior spiracles situated close together medially near posterior end of abdomen. Anus terminal.

The few larval descriptions that have been published for Nycteribiidae are short and incomplete. The larval stage outside the female uterus is very brief. Immediately after larviposition the third-stage larva quickly transforms into the pupal stage. Authors disagree on the proper term to be applied to the freshly laid offspring of 'pupiparous' Diptera. Many refer to this developmental stage as the larva, whereas others call it the prepupa (Marshall 1970). However, the term larva is used here for this developmental stage. Various authors have provided descriptions and some illustrations of this stage, including Osten Sacken (1881), Speiser (1901), Scott (1908), Muir (1912), Rodhain and Bequaert (1916), Falcoz (1926), Schulz (1939), Ryberg (1939, 1947), Hennig (1952), Löhrl (1953), Leong and Marshall (1968), and Marshall (1970). The above description is a compilation from several of these sources, supplemented with data from a single larva of *Basilia forcipata* Ferris that was preserved in alcohol just as the female was in the process of depositing it.

Pupa. Very similar to deposited late third-stage larva. Outline elliptic to oval (Fig. 7), strongly convex dorsally, flattened ventrally, with a narrow somewhat irregular flattened transparent rim of cuticle surrounding entire puparium. Color black to dark reddish brown; cuticle smooth and shining dorsally, becoming more reticulate ventrally toward margins; flattened ventral surface colorless and transparent, making developing adult clearly visible. Anterior half of puparium occupied mainly by operculum dorsally, outlined by a distinct suture, and bearing indications of two or three intersegmental lines; posterior half of puparium also with indications of several intersegmental lines (eight segments according to Ryberg 1947). Abdomen with one pair of widely separated spiracles situated at about posterior third of pupa and with one closely placed pair of small posterior spiracles medially.

The puparia of about 18 species of Nycteribiidae have been described (Marshall 1970). Additional papers on the puparia include those of Ferris (1930), Scott (1934, 1936), Balcells (1956), Hůrka (1963, 1964), and Theodor (1975).

Biology and behavior. As early as 1835 Westwood demonstrated the presence of a developing larva in the female abdomen of a species of '*Nycteribia*' Latreille, thus establishing that the family is viviparous. Despite this early beginning very little has been published on the biology of these flies. Until recently, only a handful of papers contained significant data on the biology of the Nycteribiidae (Rodhain and Bequaert 1916, Hase 1931, Schulz 1939, Ryberg 1939 and 1947, and Hůrka 1964). Theodor (1967) and Askew (1971) both gave a concise summary of the biology of the family, but the most significant are three recent papers on Oriental species, by Leong and Marshall (1968) and Marshall (1970, 1971), that have added greatly to our biological knowledge of these curious flies. All the above studies indicate that the life cycle is rather uniform throughout the Nycteribiidae. The following summary of a typical life cycle is taken mainly from Marshall's (1970) observations on *Basilia hispida* Theodor.

Both the male and female are sexually immature at emergence and require five or six days to reach maturity. Mature males copulate with both newly emerged females and with pregnant females that are about to deposit larvae. Mating lasts from about 30 min to 2 h. One mating is sufficient for producing numerous larvae because the two spermathecae actively store spermatozoa. The female ovaries ovulate alternately, producing one egg at a time that descends into the uterus for development following fertilization. After the egg hatches, the larva feeds and grows within the female uterus, where it is nourished by the secretions of the milk glands. Hatching occurs after about 4 days and the first-instar larva quickly passes through the first larval molt. About 3 days later the second larval molt occurs, giving rise to the third and final larval instar. About eight or nine days are required for development within the uterus. The female deposits its first larva 13 or 14 days after mating. Subsequent larvae are deposited at about 9-day intervals. All nycteribiids are obligate blood-sucking ectoparasites on bats. The female leaves its host bat just before larviposition and usually deposits the larva on a vertical surface of the bat roost. During larviposition the female moves her abdomen from side to side and extrudes the larva. The newly emerged larva is active. Its initial movement helps to spread out its ventrally folded flap or flange that serves to anchor it to the substrate. The female straddles the larva and presses it down with her thorax and abdomen, to help ensure its firm fixation to the substrate. Then she returns to the host. The larva immediately transforms into the pupal stage, achieving the final shape of the puparium within about 1 min of being deposited. Apparently during this time the neck-like structure of the larva bearing the mouth is invaginated into the anterior end of the pupa. The puparium immediately begins to harden and darken. This process takes about 2 h to complete. The puparium is usually oriented with its anterior end downward on a vertical surface. The time between larviposition and emergence of the adult varies with the species and the presence or absence of a host bat. With a host nearby this time varies from about 16 to 26 days; without a host present an adult in a puparium can remain viable for up to about 43 days, after which the unemerged adult dies. Before the adult emerges, it apparently starts to imbibe air. The internal pressure thus created, in conjunction with pressure from the action of the front legs which are folded dorsally over the head, causes the operculum to break away, allowing the adult to quickly emerge. Newly emerged adults are pale white and require about 1 day to completely harden and darken to their normal color. The total life cycle from emergence of a female to the emergence of her first offspring is about 39 days for *B. hispida*. Males and females occur in about equal numbers, are capable of feeding soon after emergence if a suitable host is located, and have a life expectancy of less than 6 weeks.

All nycteribiids, which are ectoparasitic on bats, spend nearly all their time on the host. Theodor (1967) said he had seen specimens from hosts of such mammals as *Tupaia*, pangolin, mouse deer, and *Paradoxurus*, but he considered these as cases of straggling with no biological significance.

Species of nycteribiids exhibit various degrees of host specificity. Some species are restricted to a single host species, some may be found on several host species of a single genus, others may be found on several host genera of a single family, and still others may occur on many species belonging to several different families of bats (Theodor 1957). On the other hand, Marshall (1976) believes that most species are confined to a single host species or genus, thus exhibiting a much narrower range than is generally assumed by most previous authors. Possible causal factors of host specificity mentioned by Marshall include physical isolation of the hosts, climatic restrictions of both host and parasite, competition among the various bat ectoparasites, selective predation on the flies by the host, morphological adaptation of the flies to such features as hairiness of the host, and physiological adaptations of parasite to host. Parasite distribution does not always coincide with preferred host distribution because of one or more of the above or other factors, and host associations may change in different parts of the range of the parasite. Much more attention to such factors in determining host specificity should be rewarding.

New World species of *Basilia* Ribeiro are mainly parasites on bats of the family Vespertilionidae. There are about 12 species of *Basilia* reported as parasitizing bats of the family Phyllostomatidae (Guimarães 1966, Webb and Loomis 1977), but these records are probably based on accidental associations only. *Basilia tiptoni* Guimarães and *B. mimoni* Theodor & Peterson probably are the only true parasites known on phyllostomatid bats. The primitive Neotropical genus *Hershkovitzia*, the only other New World genus, is exclusively parasitic on bats of the genus *Thyroptera* Spix (family Thyropteridae).

For more comprehensive discussions of the relationship between the host and parasite, the works of Guimarães (1972), Guimarães and d'Andretta (1956), and Wenzel and Tipton (1966) should be consulted, as well as the other references given above.

Parasites of nycteribiid flies have been briefly discussed by Corradetti (1936), for the protozoans, and Samšiňáková (1960) and Nowosad (1973), for the ascomycete fungal hyperparasites. Aschner (1946) discussed the symbiotic relationships between *Eucampsipoda hyrtlii* (Kolenati) (as *E. aegyptia* Macquart) and bacteria. He concluded that the main role of these symbionts is to supply certain vitamins to the growing nycteribiid larva, which is unable to complete growth on a diet of vertebrate blood alone. Their blood-sucking habit makes nycteribiid flies vectors of *Polychromophilus*, haemosporidian parasites of bats, particularly in the Old World (Dew and McMillan 1970, Garnham 1973).

Classification and distribution. The nycteribiid bat flies are among the most specialized of all the Diptera, and their peculiar behavior and modified morphology have aroused considerable curiosity among dipterists. Nycteribiids were not always recognized as true flies (Westwood 1835), and have had a confused nomenclature (Collins 1931). Important summaries of what was known about the family were published by Westwood (1835), Kolenati (1863), and Speiser (1901). Numerous other papers followed, treating mainly the Old World fauna. Only a few papers dealt with species of the New World. The first comprehensive treatments of the New World fauna were published by Guimarães (1946) and Guimarães and d'Andretta (1956). The latest and most comprehensive treatment of the family, essentially on a world basis, was published by Theodor (1967). Although he did not treat all the world species, Theodor's work is the most complete and useful treatment of the family yet published. Other useful papers dealing with the identification of New World species include those of Ferris (1924), Curran (1935), Guimarães (1946, 1966, 1972, 1977), Peterson (1960, 1971), and Whitaker and Easterla (1974). The family was first recorded from Canada by Spencer (1938). Stiles and Nolan (1931) and Wenzel (1965) provided lists of the Nearctic species. Guimarães (1968), Maa (1977), and Hutson and Oldroyd (1980) provided catalogs of extralimital species. Maa (1965) provided an interim world list of the described species and in 1971 he published a useful bibliography of papers published to the end of 1970.

According to Theodor (1967, 1975) the family is divided into the subfamilies Nycteribiinae (primarily parasites of bats of the suborder Microchiroptera) with six genera, and the Cyclopodiinae (primarily parasites of bats of the suborder Megachiroptera) with five genera. The most recent and perhaps the most controversial classification was that of Griffiths (1972), who placed the Nycteribiidae, along with the Streblidae, in the family Hippoboscidae as the subfamily Nycteribiinae. Griffiths' scheme is not followed here.

To date, about 256 species have been described in 12 genera. The family is world wide in distribution exclusive of the Arctic areas, with the majority of species occurring in the warmer regions. The family is believed to have had its center of origin in the Malaysian subregion. The New World species of *Basilia* are assumed to have originally entered the area with vespertilionid bats. Their closest relatives are believed to be Old World species of *Basilia* belonging to the *B. bathybothyra* Speiser group, which today is mainly tropical in distribution (Theodor 1957). *Basilia* is the only genus that contains species in both the Old and New worlds. The two New World genera, *Basilia* and *Hershkovitzia*, belong to the subfamily Nycteribiinae. *Hershkovitzia* is strictly Neotropical, with four described species. *Basilia* has about 42 New World species, of which seven have been reported in North America. There are no fossil records for the family.

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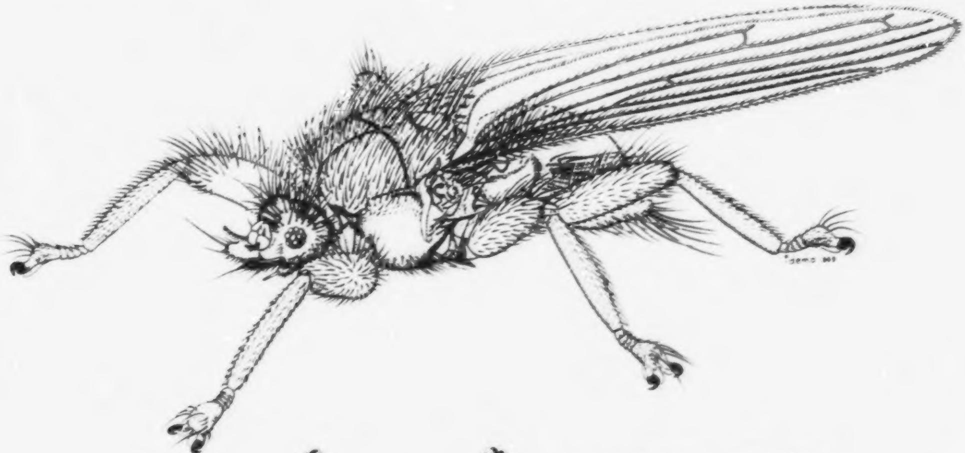
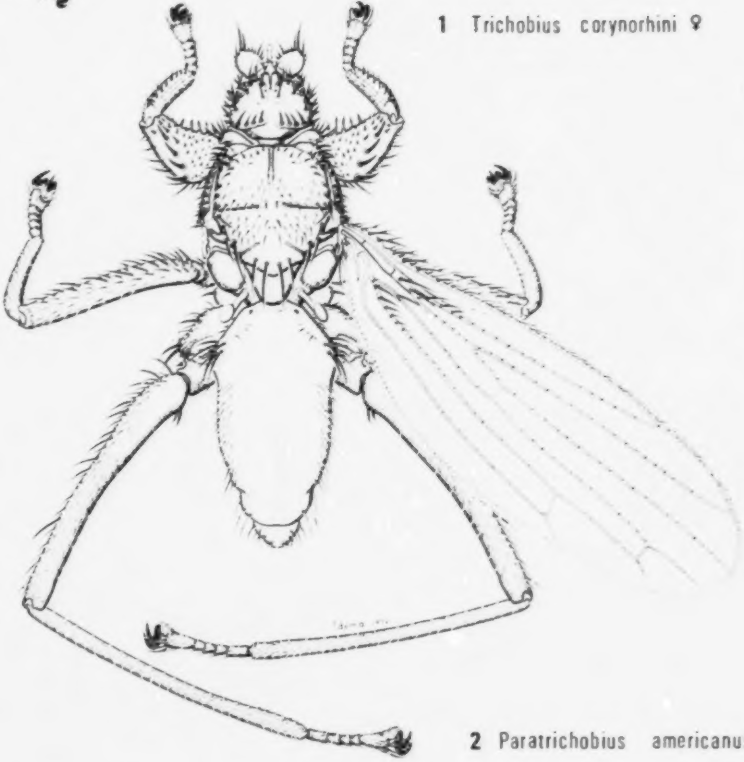
STREBLIDAE

113

RUPERT L. WENZEL AND B. V. PETERSON



1 Trichobius corynorhini ♀



2 Paratrichobius americanus ♂

Figs. 113.1–2. Adults: (1) female of *Trichobius corynorhini* Cockerell; (2) male of *Paratrichobius americanus* Peterson & Ross.

Mostly small 'pupiparous' blood-sucking flies (Figs. 1, 2), ectoparasitic on bats, often rather densely setose. Length averaging 1.5–2.5 mm, but a few Neotropical species ranging from 0.75 mm to 5.0 mm. Form varying from generalized convex to laterally compressed and flea-like, to dorsoventrally flattened and polyctenid-like. Head of some species with a ventral ctenidium. Abdomen extensively membranous, with a corresponding reduction or loss of sclerites. Most species with fully developed wings, but some brachypterous, stenopterous, or apterous.

Adult. Head: usually small, somewhat rounded and funnel-shaped in dorsal view (Fig. 2), but often somewhat flattened dorsally (Nycteriboscinae, Trichobiinae), or laterally compressed (Nycterophiliinae), or strongly flattened dorsoventrally and polyctenid-like (Streblinae and some Old World species), with conspicuous setae and bristles except on face (frontoclypeus); a ventral postgenal ctenidium present in Streblinae and in the New World genus *Eldunnia* Curran, possibly serving to protect the membranous mobile joint between the head and thorax from abrasive action of the host's hairs (Marshall 1980*b*). Dorsum of head consisting mostly of face anteroventrally and frons dorsally; frons sometimes divided, at least along midline, to form two distinct fronto-orbital plates (laterovertices) bearing eyes laterally; face and usually fronto-orbital plates separated from other regions of head by membrane; vertex (postvertex) in form of a small isolated median setose plate, or fused with fronto-orbital plates and forming a pair of convex or somewhat flattened lobes (occipital lobes) (Trichobiinae), or forming a flattened bilobate occipital plate whose posterior margin is festooned with strong usually spine-like setae and bristles (Streblinae); ptilinum vestigial, not sac-like, represented by a narrow membrane. Eyes greatly reduced, usually with 7–11, but sometimes 28–36, facets in New World species, or with a single facet or none at all in a few American and most Old World species; ocelli absent. Antenna inconspicuous; scape fused with head capsule; pedicel with a dorsal furrow; flagellum pyriform or oval in shape and mostly concealed within pedicel, bearing a distally pectinate arista. Mouthparts of piercing–sucking type with labium modified and externally consisting of a bulbous or pyriform prementum (labial theca) basally and a needle-like process distally ending in tiny labella; palpus single-segmented, foliaceous, oval or triangular in shape, setose on margins and outer (ventral) surface (Fig. 1) (Trichobiinae), or much enlarged, prominent, and covered with strong or even spiniform setae along external margins and on ventral surface, sometimes with both palpi meeting along midline to form a prominent shield for anterior portion of head (Streblinae).

Thorax: varying from convex and subglobose, or subquadrate and slightly convex (Figs. 1, 2) (Trichobiinae), to strongly flattened or compressed dorsoventrally (Streblinae), or strongly compressed laterally (Nycterophiliinae). Pronotum greatly reduced, scarcely recognizable; postpronotal lobe not differentiated. Scutum with a complete or incomplete transverse suture; this suture usually strongly sclerotized, rarely membranous; presutural area of scutum (prescutum of most authors) with a longitudinal median suture; this suture usually variously incomplete, but sometimes united with transverse suture, and absent only in Nycterophiliinae and in Old World genera; scutellum usually well-developed, with its distal margin angulate in New World genera and rounded in Old World genera. Notopleural suture and anepisternal (vertical) cleft usually open and membranous, but sometimes closed and rigid or partially so; laterotergite of postnotum usually well-developed, but much reduced in flightless species. Disc of scutum setose; setae sometimes varying greatly between species in density, length, and distribution; scutellum with one to eight (rarely 10), usually four, long setae in New World species; postnotum bare; pleural sclerites mainly bare.

Legs variable in length and stoutness; hindleg usually distinctly longer than others (Fig. 2), sometimes greatly elongated, and clothed with long and short setae. Tibia without apical spurs, although peculiar bifid spur-like setae present in *Nycterophilia* Ferris. Claws usually large and simple, but adapted for clinging; pulvilli pad-like; empodia simple and somewhat flattened or feathered, rarely branched.

Wing (Figs. 1–4) of most species of American genera, when fully developed, moderately large, usually slightly smaller in male, at rest lying flat over abdomen (Fig. 1); membrane without markings, although usually densely covered with microtrichia; veins usually with short to moderately long setae above and below, and with longer setae on C and basal portions of some longitudinal veins and sometimes on R_1. C ending at tip of R_{4+5}; Sc usually short and represented by a faint colorless line often lying close to R_1, sometimes absent or, as some authors suggest, possibly fused with R_1, at least basally; R_1 joining C at about distal third of wing; R_s branching at about basal third; R_{2+3} joining C near apex; R_{4+5} joining C at apex of wing; crossvein r-m usually situated a little before midlength of wing; M_{1+2} reaching or nearly reaching wing margin; crossvein dm-cu situated near apex of wing; CuA_1 and CuA_2 with a long common petiole; CuA_2 branching off at about distal two-thirds (just beyond midlength of wing), running free for a short distance and then joining A_1 near margin of wing and reaching it as $A_1 + CuA_2$; A_1 long; A_2 very short, evanescent distally; CuP not evident. Alula absent. Calypter club-shaped, setose. Some species brachypterous or stenopterous, with variously reduced venation, occasionally apterous. Wing longitudinally folded in *Nycterophilia*, with only three well-developed anterior longitudinal veins (Fig. 4); M_{1+2} evanescent beyond crossvein r-m and continued to apex of wing as a setose line along a wing fold; eight or nine other indistinct longitudinal vein-like lines of setae also present. Wing of Old World genera (Nycteriboscinae) with slightly reduced venation and usually with a distinct alula, longitudinally folded at rest and lying along dorsum of abdomen between longitudinal bands of strong curved setae situated on each side of dorsal membrane of abdomen. Wing of Ascodipterinae with only three longitudinal veins and no crossveins; R_{2+3} reduced; M_{1+2} and A indicated by membranous folds.

Abdomen: mostly membranous and somewhat sacciform (Figs. 2, 5, 6), especially in gravid females; syntergite 1 + 2 large, heavily sclerotized, basically subquadrate to subrectangular in shape, with each posterolateral corner (which is usually subdorsal in position) developed lobe-like; hind margin between these two lobes either straight or variously emarginate; each lobe bearing stout bristles and usually a variable array and pattern of setae anteriorly and medially. Tergite 1 component of syntergite 1 + 2 sometimes separated from tergite 2 by a thin but distinct suture and sometimes indistinguishably fused, usually bearing anterior pair of spiracles; spiracle 2 usually present in posterolateral lobe or in membrane just lateral and ventral to each lobe. Spiracles 1–7 present in New World genera, 2–7 in Nycteriboscinae, and 5–7 in Ascodipterinae. Sternite 1 and 2 separate; sternite 1 sometimes absent (*Raymondia* Frauenfeld), but usually occurring as a short single bar-like sclerite, although sometimes appearing longer and plate-like, or divided into two lateral plates, or present in the form of a single plate that is narrowed medially and variably expanded plate-like laterally, usually bare medially and with various setae laterally. Sternite 2 usually large and distinct, varying in shape from rectangular to subquadrate to subtriangular or cordiform, bare anterolaterally, variably setose posteromedially; an anteromedian longitudinal suture-like weakening sometimes evident. Tergites 3–6 and sternites 3 and 4 usually not sclerotized in either sex; all sternites sclerotized in male Nycterophiliinae; tergite 6 occasionally present in at least some males of Nycteriboscinae as two dorsolateral setose plates, and in a few males of *Trichobius* Gervais as a narrow transverse faintly sclerotized setose strip; in some species abdominal segments 3–6 or 3–7 are indicated by a row or patch of fine or coarse setae or by a transverse bare strip.

Female (Figs. 5, 6) with tergite 7 often present as a small median sclerite or as two separate lateral plates bearing various setae, or sometimes fused with epiproct; tergite 8 membranous, or perhaps fused with epiproct (supra-anal plate of previous authors); epiproct usually cone-like, somewhat variable in size and form, bearing both short and long setae. Cerci small, free or fused with epiproct, sometimes fused with hypoproct (ventral arc). Sternite 7 absent, or present as two sublateral plates bearing various combinations of short and long setae; sternite 8 membranous, or present as a small to prominent single midventral plate, or as two submedian sclerotized plates; these plates bare or setose. Hypoproct often well-developed, usually forming a heavily sclerotized U-shaped, ridge-like or trough-like structure (ventral arc of previous authors) that, in turn, may be fused with the epiproct or articulated with it. Hypoproct sometimes consisting of two or three distinct sclerites that are usually connected, even if tenuously; hindmost piece often present as a separate tiny sclerite bearing a pair of setae. Spermathecae not definitely known but probably present as two short tubular or sac-like structures similar to those of Nycteribiidae, in *Ascodipteron speiserianum* Muir possibly present as two small glands opening at base of oviduct (Muir 1912).

Male abdomen with sternite 5 present or absent, but when present, usually well-developed as a large single or divided setose plate and sometimes greatly reduced as two short narrow sclerotized strips. Male terminalia (Figs. 7, 8) retractable, usually concealed at rest, but mostly exposed in Nycterophiliinae and Ascodipterinae (Old World). Abdominal segments 7 and 8 rotated 180°; segment 9 rotated a full 360° (Jobling 1951).

Sternite 6 absent, or occasionally present and well-developed, or as a faintly sclerotized narrow setose strip, or sometimes partially fused with sternite 7 yet partially separated by a distinct suture. Tergite 7 sometimes fused over most of its area with syntergosternite 8 and with a varyingly distinct remnant of sternite 7 ventrally; sternite 7 sometimes complete ventrally as a narrow ring-like structure attached dorsally on each side to syntergosternite 7 + 8; an anterior spur-like plate occasionally present on each side ventrally, possibly representing remnants of sternite 6; spiracle 7 usually located dorsolaterally in anterior portion of syntergosternite 7 + 8, but some Nycteriboscinae with spiracle 7 located in membrane at each end of a faintly sclerotized narrow transverse bar-like tergite 7; in latter case syntergosternite 8 either entirely absent, membranous, or fused with tergite 9, the epandrium. Epandrium often large and funnel-like (an inverted cone) or sometimes considerably reduced, sometimes composed solely of tergite 9, sometimes partially or completely fused with epiproct, and sometimes fused with syntergosternite 7 + 8 or only with syntergosternite 8, or varying combinations of these segments. Cerci small but distinct, usually free. Epiproct variously developed, sometimes fused with complex sclerite forming epandrium, sometimes separate and distinct, and sometimes indistinctly separated from epandrium, always articulating ventrally with hypoproct. Sternite 10 sometimes spade- or diamond-shaped, or forming a dorsoventrally oriented narrow bar-like sclerite articulating dorsally near ventral margin of cercus and ventrally on left side only with hypandrium (Nycteriboscinae), sometimes reduced to two vertical plates, one on each side of genital opening, where they articulate with each side of hypandrium (some Trichobiinae). Surstyli weakly developed except in Nycterophiliinae (Fig. 8) and *Brachytarsina* Macquart; in latter genus each surstylus short but distinct, and bearing two long setae; in some Trichobiinae and Streblinae surstyli represented by small sclerotized setose plates or small patches of setae. Hypandrium, or sternite 9, with a relatively long anteromedian apodeme and distally continuous with two digitiform gonopods; gonopod bearing ventrally near its point of origin two setae, one of which is usually long and the other shorter (often much shorter), also with various minute sensory setulae; in Trichobiinae and Streblinae (New World), gonopods usually symmetric but these sometimes asymmetric, or with one gonopod usually greatly reduced (*Raymondia*, Old World); hypandrium variably closed dorsoposteriorly, forming a trough or sheath through which aedeagus passes; a roof-like plate comprising anterodorsal margin, extending from base of each gonopod to base of aedeagus, possibly representing fused parameres; posterodorsal margin with an inverted U-shaped hypandrial bridge present articulating ventrally with sternite 10; aedeagus long and slender, distally ribbon-like, flagelliform, or blade-like, coiled or partially coiled basally in most New World species; aedeagal apodeme usually long and slender, as long as or longer than hypandrial apodeme. In Nycterophiliinae, terminalia exposed (Fig. 8); epandrium large, elongate, bifurcate with two long tapering ventrally directed shaft-like extensions, each bearing distally a short movable digitiform surstylus whose chaetotaxy is similar to that in other streblids; a relatively large elongate hypandrium present, lying between shaft-like extensions of epandrium, strongly tapered ventrally and continuous distally with a pair of very short partially separated gonopods; aedeagus long, tube-like, bulbous basally, not coiled, tapering distally; aedeagal apodeme long.

Additional works on the morphology of adult Streblidae include those of Jobling (1929, 1936, 1939*a*, 1951), Zeve and Howell (1962, 1963*a*, *b*), Wenzel *et al.* (1966), Schlein (1970), Schlein and Theodor (1971), and Hennig (1971). According to Cooper (1941) the 2*n* chromosome number of seven genera and species of Streblidae studied was 10.

Puparium. The puparia of only a few species have been described and illustrated. In the New World there are three basic types of puparia corresponding to subfamily divisions.

Trichobiinae (Fig. 10): yellowish to dark brown, oval, broadly oblong oval, or suborbicular, convex above and flattened below, with a well-defined operculum on anterior half or slightly less. Venter varying from nearly membranous and translucent to distinctly pigmented and hardened, attached to substrate along margins; dorsum variously reticulate, tuberculate, setose, or with numerous small more heavily pigmented areas; cuticle sometimes with transverse straight or curved concentric ridges (possibly segmental lines). Typically with two pairs of spiracles present on posterior third or quarter, variously situated on one or two prominences or on separate tubercles; anterior pair of spiracles usually larger and more widely separated than posterior pair and sometimes situated far anterior to these; posterior pair represented by a single large spiracle in *Noctiliostrebla* Wenzel; a median respiratory pore often visible near posterior end of venter.

Nycteriboscinae (confined to Old World): known puparia are similar to those of Trichobiinae.

Nycterophiliinae: puparium almost smooth, nearly egg-shaped, slightly narrower in dorsal view; distinctive opercular line absent. A single pair of small widely separated spiracles present at posterior end.

Streblinae: shape similar to that of Trichobiinae, but evenly pigmented and hardened throughout, nearly smooth, without well-defined ventral margins, though flattened and feebly concave below. Spiracles absent, but 130–140 respiratory pores present, opening externally through cuticle from a pair of tracheae lying just below integument; tracheae approximated and united at posterior end of puparium, then extending anteriorly on each side following either a much convoluted course along venter, sides, and dorsum or a more direct course about halfway between midline and sides; together these forming a dorsomedial anteriorly or posteriorly directed loop behind opercular line; a single isolated median pore present, situated near apex of venter. A heavily sclerotized hook-shaped structure (possibly a mandible) evident as a black dot through venter of puparium just posterior to opercular line.

Illustrations of puparia of several New World genera are given by Ferris (1923) and Guimarães (1944) and for a few Old World species by Ryberg (1947), Theodor and Moscona (1954), and Theodor (1968).

Biology and behavior. Streblidae are obligate hematophagous parasites of bats. All are ectoparasitic except for the females of the Old World genus *Ascodipteron* Adensamer which embed themselves in the skin of the host, lose their wings and legs, and undergo neosomatic changes (Audy *et al.* 1972) to become sacciform endoparasites.

Streblidae are adenotrophic and viviparous. Their larvae develop one at a time, nourished by uterine milk glands. Little is known of the development time between fertilization and deposition of the larva. Observations by Overal (1980) indicate that the female of *Megistopoda aranea* (Coquillett) produces at most one larva every 10 days. Immediately after the larva is deposited, its cuticle tans and hardens to form a puparium. Some species have communal deposition sites; the female of these species leaves the host and deposits its larva in a flat depression or a wide flat crevice (Ross 1961). The larva of *Ascodipteron* falls to the ground and pupates below the host's roost. Puparia of *Trichobius major* (Coquillett) may occur abundantly on walls of caves in which the hosts roost. In Trinidad, J. Darlington (personal communication) found viable as well as empty puparia of *Trichobius caecus* Edwards so abundant that they formed a crust on the walls of a cave chamber apart from the roosting area of the bats.

In *Ascodipteron rhinolophi* Jobling the duration of the pupal stage is 35–37 days at 27°C (Theodor and Moscona 1954). In *Megistopoda aranea* this stage was found to last 22–24 days at 100% relative humidity and 18°C; the average adult life span was 29 days, with mortality resulting primarily from such causes as disassociation and grooming and predation by the host rather than senescence (Overal 1980). Ross (1961) and Wenzel *et al.* (1966) found that adults of the New World species they observed did not survive more than 1 or 2 h when removed from the host. However, Overal (1980) kept disassociated engorged adults of *M. aranea* alive for 3–20 h and teneral unfed adults for 18–38 h at 18°C and 100% relative humidity.

Observations by Ross (1961) and Overal (1980) indicate that newly emerged adults must feed before mating, that previously gravid females may mate numerous times, and that mating is probably necessary after each larval deposition in order to fertilize the next ovum. This behavior perhaps indicates that the spermathecae are either nonfunctional or absent.

Streblids often occur on colonial, cave-dwelling bats, but most species of New World Streblidae occur on bats that roost in forest habitats. Typically they are absent from solitary-roosting bats. Bats in well-established roosts tend to have more streblids than those in newer roosts. Most New World species are host-specific (monoxenous) or occur on two or more closely related hosts. A few are polyxenous and, especially in the temperate zones, occur on taxonomically unrelated hosts that roost in the same site. Adults of most fully winged New World streblids, although highly mobile, remain closely associated with the host. Some, however, like *Trichobius caecus*, may be seen flying in large swarms in cave-roosting sites. The various species tend to have preferred sites on the host bat (Ross 1961, Wenzel *et al.* 1966, Marshall 1980*a*, Overal 1980). Some temperate North American species, like *Trichobius major* and *T. corynorhini* Cockerell, overwinter on hibernating bats in caves where there is freely circulating air (Zeve 1959). Locomotion of streblids is remarkable in that they can move in any direction with equal facility. This mobility is especially noticeable when they are on the wing membranes of the host. *Megistopoda aranea* pushes through the fur with its long hindlegs (Overal 1980). Flightless species occur primarily on fish-eating and fruit-eating bats. Flightless species tend to have a more equally balanced sex ratio than fully winged species, and in seasonal areas there is some evidence to suggest a seasonal variation in the sex ratio of some species (Marshall 1981).

Streblidae feed frequently (Wenzel *et al.* 1966, Overal 1980). Most species die within about 24 h if deprived of food (Marshall 1980*a*). Occasionally, species of *Trichobius* have been known to bite man (Eads *et al.* 1957, Ross 1961). Wenzel (unpublished observation) experienced bites on his hands by *T. macrophylli* Wenzel after he had acquired the odor of the hosts through handling them. Kessel (1924) reported a few stray individuals on doves, parrots, and an opossum, but these records are almost certainly in error.

For additional information on biology and the relationship between host and parasite see works by Jobling (1949), Theodor (1957), Ross (1961), Wenzel *et al.* (1966), Audy *et al.* (1972), Webb and Loomis (1977), Marshall (1980*a*, 1980*b*, 1981), and Overal (1980).

Classification and Distribution. The family Streblidae was proposed by Kolenati in 1863 for the genera *Brachytarsina* and *Raymondia* (Old World) and *Strebla* Wiedemann (New World). Speiser (1900) recognized two subfamilies: Streblinae for *Strebla sensu* Speiser, 1900 (=*Anastrebla* Wenzel, 1966) and *Euctenodes* Waterhouse (=*Strebla* Wiedemann), and Nycteriboscinae for all other Old and New World genera. Kessel (1925) followed Speiser and, interestingly, included *Nycterophilia* in the Nycteriboscinae. Jobling (1936) proposed the subfamily Trichobiinae for most New World genera including *Nycterophilia*, reduced the family Ascodipteridae to a subfamily of Streblidae, and redefined the Streblinae to include *Pseudostrebla* Costa Lima, *Eldunnia*, and later (Jobling 1939*b*), *Stizostrebla* Jobling. Wenzel *et al.* (1966) reassigned these latter genera to the Trichobiinae. Wenzel *et al.* (1966) proposed an additional subfamily, Nycterophiliinae, for the genus *Nycterophilia*, and later Wenzel (1976) also added *Phalconomus* Wenzel (as *Phalcophila* Wenzel, not Brennan and Reed). A very different classification is that of Griffiths (1972), who included the Pupipara in the single family Hippoboscidae, with two subfamilies, the Hippoboscinae (Hippoboscidae auct.) and the Nycteribiinae (Streblidae and Nycteribiidae, as tribes). Hennig (1973) retained the traditional family rankings but recognized only two subfamilies of Streblidae, the Nycteriboscinae (=Ascodipterinae) and the Streblinae (=Nycterophiliinae, Trichobiinae). The treatment used here follows that of Jobling (1936), as modified by Wenzel *et al.* (1966) and Wenzel (1976). We recognize two Old World subfamilies, the Nycteriboscinae (5 genera, 54 spp.) and the Ascodipterinae (1 genus, 18 spp.), and three New World subfamilies, the Nycterophiliinae (2 genera, 6 spp.), the Trichobiinae (19 genera, 111 spp.), and the Streblinae (4 genera, 32 spp.). Apart from the distinctive morphology of the adults, the New World subfamilies are further characterized by striking differences in the puparia. The status of the Streblidae and other Pupipara is discussed by Theodor (1964), Hennig (1965, 1971), Griffiths (1972), Schlein (1970), and Wenzel (1976).

Most species of Streblidae, like their host bats, occur in the tropical and subtropical regions of all continents and on many islands of the Indian and Pacific oceans. A few species occur in temperate regions. According to Jobling (1951) they are basically limited to those areas lying between latitudes 40°N and 40°S. In North America, *Trichobius corynorhini* occurs as far north as British Columbia in the west and West Virginia in the east. Nine species in three genera are known from the United States and Canada. It is possible, however, that the genus *Strebla* might be found on bats along the northern parts of the coast of the Gulf of Mexico or even in southeastern Texas.

For identification of North American taxa, see works by Jobling (1938, 1939*c*), Ross (1959), Peterson and Ross (1972), Whitaker and Easterla (1974), Wenzel *et al.* (1966), and Wenzel (1976). Extralimital works include those of Jobling (1930, 1934, 1939*c*, 1951, 1954), Theodor (1954, 1968, 1975), Wenzel *et al.* (1966), Maa (1967, 1971*a*, 1971*c*), Peterson and Hůrka (1974), and Cuy (1980). Catalogs and lists include those of Maa (1965, 1977), Wenzel (1965, 1970), Webb and Loomis (1977), and Hutson and Oldroyd (1980). A comprehensive annotated and classified bibliography was given by Maa (1971*b*). There are no known fossils of Streblidae.

Keys to genera

Adult

1. Body strongly compressed laterally, flea-like. Wing subtriangular, narrow basally, broadened distally, with only three distinctly sclerotized veins, and with a medial notch in distal margin (Fig. 4). Male with sternites 1–6 well-developed and sclerotized; terminalia (Fig. 8) external, not retractable into abdomen .....NYCTEROPHILIINAE....***Nycterophilia*** Ferris

2 spp.; southwestern U.S.A.

Body broader and flatter dorsoventrally, if somewhat compressed laterally then never flea-like (Figs. 1, 2). Wing normal in shape, with six distinct longitudinal veins and without a notch in distal margin (Fig. 3). Male with sternites 3 and 4 never sclerotized; terminalia (Fig. 7) retractable into abdomen 2

2. Head with a ventral postgenal ctenidium consisting of numerous spines and extending around sides to dorsolateral parts of head. Palpus very broad, covered with numerous short stout spines; together, palpi forming a broad shield for front of head ....STREBLINAE....***Strebla*** Wiedemann

Neotropical, but possibly occurring on Mexican plateau

Head without a postgenal ctenidium. Palpus sometimes broad but always free with normal setae; together palpi not forming a broad shield for front of head .....TRICHOBIINAE....3

3. Inner surface of fore femur without strong spine-like setae; hindleg shorter, not conspicuously elongate; hind tibia not flexible but uniformly sclerotized and pigmented (Fig. 1)..***Trichobius*** Gervais

5 spp.; British Columbia southward in the west and from Kentucky southward in the east

Inner surface of fore femur with a diagonal row of heavy spine-like setae; hindleg greatly elongated; hind tibia flexible, with numerous minute unpigmented or weakly sclerotized transverse cracks or spots (Fig. 2) ....***Paratrichobius*** Costa Lima

1 sp., *americanus* Peterson & Ross; Arizona

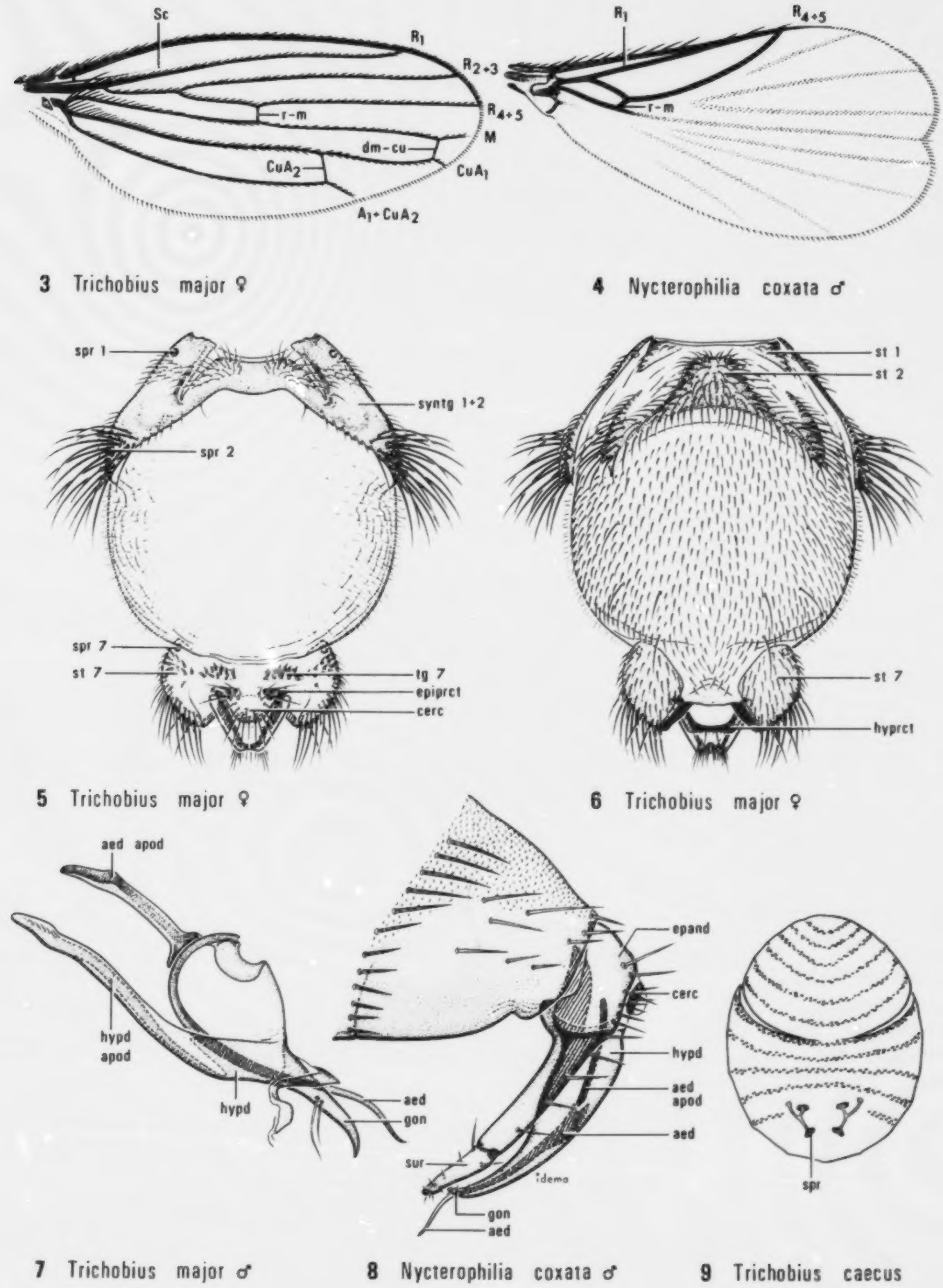
Puparium

1. Spiracles absent, but with a series of 130–140 respiratory pores; pores opening externally through cuticle from a pair of tracheae that unite at posterior end of puparium; tracheae extending anteriorly on each side, together forming a dorsomedial anteriorly or posteriorly directed loop behind opercular line ....***Strebla***

One or two pairs of posterior spiracles present 2

2. Form seed- or egg-shaped in both dorsal and lateral views, without a distinctive ventral margin; cuticle uniformly hardened and pigmented throughout; a distinctive opercular line absent and no surface ornamentation evident. One pair of small widely separated spiracles present at posterior end ....***Nycterophilia***

Form oblong oval to nearly round in dorsal view, convex above, flattened and sometimes shallowly concave below, with rather sharp ventral margin; cuticle usually less hardened and less strongly pigmented ventrally than dorsally; dorsal surface usually ornamented with reticulations, setae, or tubercles. Two pairs of posterior spiracles present (Fig. 10) ....***Trichobius***


Sc
R1
R2+3
r-m
R4+5
M
dm-cu
CuA2
CuA1
A1+CuA2
R1
R4+5
r-m
spr 1
syntg 1+2
spr 2
spr 7
st 7
tg 7
epiprct
cerc
st 1
st 2
st 7
hyprct
aed apod
hypd apod
hypd
aed
gon
epand
cerc
hypd
aed apod
aed
sur
gon
aed
idemo
spr

3 Trichobius major ♀

4 Nycterophilia coxata ♂

5 Trichobius major ♀

6 Trichobius major ♀

7 Trichobius major ♂

8 Nycterophilia coxata ♂

9 Trichobius caecus

Figs. 113.3–9. Wings, abdomens, terminalia, and puparium: wings of (3) *Trichobius major* Coquillett and (4) *Nycterophilia coxata* Ferris; (5) dorsal view and (6) ventral view of abdomen of female of *Trichobius major*; left lateral views of male terminalia of (7) *Trichobius major* and (8) *Nycterophilia coxata*; (9) puparium of *Trichobius caecus* Edwards (not Nearctic) in dorsal view, redrawn from Guimarães 1944.

Abbreviations: aed, aedeagus; aed apod, aedeagal apodeme; cerc, cercus; epand, epandrium; epiprct, epiproct; gon, gonopod; hypd, hypandrium; hypd apod, hypandrial apodeme; hyprct, hypoproct; spr, spiracle; st, sternite; sur, surstylus; syntg, syntergite; tg, tergite.

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CORRECTIONS AND ADDENDA TO VOLUME 1

Chapter 2. Morphology and Terminology—Adults

p. 14, col. 2, line 18 Change "parafacials" to "parafacial"

p. 15, col. 2, line 17 Insert the title "**Gena and Subgena**" to head the paragraph beginning "The region between the lower margin of the eye"

p. 15, col. 1, line 2 Change "Fig. 25.46" to "Fig. 25.2–4"

p. 16, col. 1, line 48 Change "**Johnson's organ**" to "**Johnston's organ**"

p. 17, caption for Fig. 20 Insert "flagellomeres 1–3 only" after "(Osten Sacken)"

p. 25, col. 2 After the first sentence insert:
"The suture or cleft separating the notopleuron from the anepisternum is called the **notopleural suture** (Crampton 1942, p. 48)."

p. 25, col. 2, line 12 Change "scutellum" to "postalar callus"

p. 26, Fig. 65 Change the label "psut sct" to "psut area"

p. 26, Fig. 66 The label line for "gn dil" (genal dilation) should point to the haired part of the gena

p. 27, caption for Figs. 65–66, col. 1 Insert "fr plt, frontal plate" after line 22

p. 27, caption for Figs. 65–66, col. 3, line 13 Change "psut sct, postsutural scutum" to "psut area, postsutural area"

p. 30, Fig. 69, vein M There are inconsistencies throughout Volume 1 in the naming of M where that vein is unbranched. It is usually referred to as M or M_1, but sometimes as M_{1+2}

p. 31, col. 1, line 15 Insert "Hamilton 1971" inside the parentheses before "Kukalova-Peck 1978"

p. 31, caption for Figs. 67–69, col. 3, note marked by * Change the last mention of "m-cu" to "dm-cu"

p. 32, col. 2, line 48 Change "Tabanomorpha, Asilomorpha," to "Tabanomorpha and Asilomorpha" and delete ", and Muscomorpha"

p. 35, col. 1, line 10 Insert parentheses around "Coquillett"

p. 35, col. 1, paragraph 3, line 7 Change "raptoral" to "raptorial"

p. 45, col. 1, line 10 from the bottom of the page After "taxonomic characters." insert:
"The male genital segment, segment 9, is sometimes referred to as the andrium; thus, the terms epandrium and hypandrium, respectively, are usually adopted, especially in the Muscomorpha, for its tergite and sternite."

p. 50, Figs. 134 and 135 Change "st 8" to "syntgst 7 + 8"

p. 53, col. 2, paragraph 2, line 13 After "(Hennig 1976*b*)." insert:
"These structures are probably not homologous. In the Nematocera and most orthorrhaphous Brachycera, the so-called aedeagal apodeme arises directly from the basiphallus, but in the Muscomorpha the aedeagal apodeme arises from the aedeagal guide. Possibly the separate ejaculatory apodeme characteristic of some Stratiomyidae and all Muscomorpha is at least partially homologous with the so-called aedeagal apodeme of the lower Diptera, but in the higher Diptera the aedeagal apodeme and the ejaculatory apodeme have completely different origins."

p. 54, col. 1, line 8 from bottom of the page Delete "incorrectly"

p. 54, col. 2, line 3 from the bottom of the page Change "Xylophagidae" to "Xylomyidae"

p. 55, col. 2, lines 2 and 19 Change "processi" to "processus"

p. 58, col. 2 lines 20 and 21 from the bottom of the page Change "Figs. 127–128" to "Figs. 127–129"

p. 59, col. 2, line 13 Insert "of" after "formation"

Chapter 3. Morphology and Terminology—Larvae

p. 68, col. 1, line 21 from the bottom of the page Change "abuttment" to "abutment"

p. 72, col. 1, line 7 from the bottom of the page Change "host" to "prey"

p. 80, col. 1, line 18 from the bottom of the page Change "that" to "than"

Chapter 4. Key to Families—Adults

p. 97, couplet 30*b* Change "41" to "42"

p. 97, Fig. 37 Extend the label line for bm-cu to crossvein bm-cu

p. 99, couplet 41 Delete entire couplet

p. 99, couplet 42 Change "42." to "42 (30)."

p. 103, Fig. 70 Change "CuA_2" to "CuA_1"

p. 104, couplet 65*a* Change "Opsodexiinae" to "Angioneurini"

p. 105, couplet 72*b* After "Milichiidae" insert "and Chloropidae"

p. 105, couplet 73*a* After "ocelli" insert "and mid coxal prong"

p. 105, couplet 73*b* Change "Ocelli present." to "Ocelli usually present; if absent, mid coxal prong present."

p. 105, couplet 75*a* Insert the footnote numeral "2" after "minute" and place the following footnote at the bottom of the page:

"[2]*Loewimyia* Sabrosky (Asteiidae), from Florida and Texas, keys here; it differs from Cryptochetidae in having the first flagellomere short, compound eye small and bare, scutellum small and bare, and body much more slender."

p. 105, couplet 75*b* After "well-developed" insert "except on *Loewimyia* (Asteiidae)"

p. 115, couplet 91*b* Change "92" to "92A"

p. 115, following couplet 91 Insert couplet 92A, as follows:

"92A. Postocellar bristles convergent or absent. Clypeus small and withdrawn. Female with flexible tubular ovipositor. Mostly small gray or silvery pruinose flies .... **Chamaemyiidae** (Ch. 88)

Postocellar bristles divergent or absent. Clypeus large and prominent. Female with rigid shaft-like ovipositor. Size and color variable ...... 92B"

p. 115, couplet 92 Change "92" to "92B"

p. 115, couplet 92B*b* Change "always with four" to "always with at least four"

p. 117, Fig. 159 Change the label and caption to "*Arachnidomyia aldrichi*"

p. 119, couplet 114*a* After "convex" insert "except in *Platygymnopa* Wirth"

p. 119, couplet 114*a* Change the last sentence to: "Postocellar bristles absent; pseudopostocellar bristles, if present, divergent (Fig. 155)."

p. 119, couplet 114*b* Insert "present," after "Postocellar bristles"

p. 119, couplet 116 Change to:

"116. Katepisternum without an outstanding bristle, though frequently setulose (Figs. 106, 107). Vibrissa absent and gena without a vibrissa-like bristle (Figs. 106, 107). Mostly slender, fragile flies with elongate wings 117

Katepisternum with one or more outstanding bristles. Vibrissa present (Figs. 113, 119–122) or absent; gena with or without vibrissa-like bristle. Form variable .... 118"

p. 122, couplet 127*b* Insert the footnote numeral "1" after "absent" and insert the following footnote at the bottom of the page:

"[1]A pair of divergent pseudopostocellar setulae, present in some Tethinidae, are easily confused with true postocellar bristles (absent in Tethinidae)."

p. 122, couplet 132*a* Insert the footnote numeral "2" after "suture" and insert the following footnote at the bottom of the page:

"[2]The V-shaped suture is obliterated in the tipulid genus *Chionea* Dalman (Byers, R. W. 1983. The crane fly genus *Chionea* in North America. Kans. Univ. Sci. Bull. 52: 59–195). The relatively large size (about 5 mm), characteristic habitus, and tendency for loss of legs in preserved specimens distinguishes this genus from the remaining families."

p. 124, couplet 149*b* Change "150" to "149A"

p. 124, following couplet 149 Insert couplet 149A as follows:

"149A. Posterior thoracic spiracle with one or more fine bristles on lower margin. Palpus vestigial .... ***Sepsidae (Themira notmani*** Curran)

Posterior thoracic spiracle without bristles. Palpus normal .... 150"

Chapter 5. Key to Families—Larvae

p. 126, couplet 13*b* Change "(Fig. 100)" to "(Fig. 14.100)"

p. 134, Fig. 27 and caption for same Change "*callosomae*" to "*callosamiae*"

p. 141, Figs. 65 and 66 Change label and captions for "*Sepsis neocyanipsea*" to "*Saltella sphondylii* (Schrank)"

p. 142, Figs. 80 and 82 Change the labels and caption to "*Cynomya cadaverina*"

p. 144, couplet 86*a* Change "(Fig. 104)" to "(Figs. 90, 105)"

p. 146, Fig. 101 Change "ac md scl" to "ac or scl"

p. 146, caption for Fig. 101 Change "ac md scl, accessory mandibular sclerite" to "ac or scl, accessory oral sclerite"

Chapter 8. Blephariceridae

p. 194, col. 2, lines 6 and 10 Change "Paltostomini" to "Paltostomatini"

Chapter 14. Mycetophilidae

p. 226, col. 2, line 9 from the bottom of the page Change "excretion" to "secretion"

p. 244, couplet 85*a*, line 2 Change "segments" to "flagellomeres"

Chapter 16. Cecidomyiidae

p. 259, col. 2, lines 2 and 3 Change "Ledomyini" to "Ledomyiini"

p. 262, caption for Fig. 29 Change "(Fallén)" to "(Felt)"

p. 264, caption for Fig. 44 Change "*Polyardis*" to "*M.* (*Polyardis*)"

p. 265, Fig. 44 Change "*Polyardis*" to "*M.* (*Polyardis*)"

p. 266, couplet 35*b* Change "(Fig. 48)" to (as in Fig. 43)"

p. 266, couplet 42*a* Change "(Fig. 38)" to "(Fig. 50)"

p. 269, couplet 54*a* After "Pritchard 1960*a*" insert "(as *Barnesina*)"

p. 270, Figs. 84 and 85 Change the labels to "*Monardia (Polyardis) adela* †" and "*Monardia (Xylopriona) toxicodendri* †"

p. 270, caption for Figs. 82–87 Change the caption for Fig. 84 to "*Monardia (Polyardis) adela* Pritchard" and for Fig. 85 to "*Monardia (Xylopriona) toxicodendri* (Felt)"

p. 272, couplet 59*b* After "(Figs. 27, 28)" insert "or absent"

p. 273, couplet 80*a* Change "7–30" to "7–42"

p. 279, couplet 85*a* Change "Felt 1915" to "Felt 1915*a*"

p. 289, couplet 179*a* Change "Ledomyini" to "Ledomyiini"

p. 290, couplet 186*b* Change "Gagné 1975*b*" to "Gagné 1975*c*"

p. 290, couplet 188, lines 1 and 3 Change "gonostylus" to "gonocoxite"

p. 291, couplet 198*b* Change ***"Brachyneura"*** to ***"Brachineura"***

p. 291, col. 2, line 4 from the bottom of the page Change "Crossby" to "Crosby"

Chapter 21. Synneuridae

p. 321, col. 1, line 8 Change "(Fig. 2.79)" to "(Fig. 4.79)"

Chapter 23. Dixidae

p. 332 and 333, Fig. 10 and caption for same Change "*Dixa*" to "*Dixella*"

p. 333, couplet 2*b* After "corona" insert "(Fig. 10)"

Chapter 29. Chironomidae

p. 438, couplet 55*a* Change "*cuneata*" to "*cuneatus*"

p. 445, couplet 101*a* Change "*downsi*" to "*downesi*"

p. 448, Fig. 106 and caption to same Change "gonst" to "goncx"

p. 455, couplet 147 Change the heading "Telomatogetoninae" to "Telmatogetoninae"

Chapter 30. Pelechorhynchidae

p. 460, col. 1, lines 11 and 12 Change "*Bequaertomyia*" to "*Pseudoerinna*"

p. 460, couplet 2*b* Change "***Bequaertomyia*** Brennan" to "***Pseudoerinna*** Shiraki"

p. 461, Fig. 2 and caption to same Change "*Bequaertomyia*" to "*Pseudoerinna*"

Chapter 33. Rhagionidae

p. 484, couplet 1*a* Change "2" to "5"

p. 484, couplet 1*b* Change "5" to "2"

Chapter 34. Xylophagidae

p. 490, couplet 3*b* After "bare" insert "(Fig. 7)"

Chapter 36. Stratiomyidae

p. 497, Fig. 36.1 Change "*barbata*" to "*barbatus*"

p. 500, couplet 1*a* Change "*Antissa*" to "*Exodontha*"

p. 500, couplet 3*a* After "James 1939*b*" insert ", Woodley 1981"

p. 500, couplet 4*a* Change "CLITELLARIINAE" to "BERIDINAE" and "***Antissa*** Walker" to "***Exodontha*** Rondani"

p. 500, couplet 4*a*, line 5 After "(as *Hexodonta*)" insert ", Woodley 1981"

p. 500, couplet 5 After "widespread" insert "; Woodley 1981"

p. 500, couplet 5, line 7 After "James 1939*b*" insert "; Woodley 1981"

p. 500, couplet 7, line 7 Change "CLITELLARIINAE" to "BERIDINAE" and "***Antissa*** Walker" to "***Exodontha*** Rondani"

p. 504, couplet 26*a* Change "*decemmaculatus*" to "*decemmaculata*"

p. 509, couplet 7*a* Change the first sentence to: "Anterior spiracle on short stalk or nearly sessile."

p. 509, couplet 7*b* Change the first sentence to: "Anterior spiracle on long stalk."

p. 511 Add the following reference: "Woodley, N. E. 1981. A revision of the Nearctic Beridinae (Diptera: Stratiomyidae). Bull. Mus. comp. Zool. Harv. 149: 319–369."

Chapter 37. Therevidae

p. 518, couplet 7 Change "mesonotum" to "scutum"

p. 521, Fig. 24 Change "ant" to "mx plp" and add the label "ant" for antenna

Chapter 40. Mydidae

p. 536, Fig. 26 Shorten the pointer line for "goncx" by a quarter of an inch

Chapter 41. Apioceridae

p. 544, col. 2, line 20 Change "Painter (1932, 1936)" to "Painter (1932, 1938)"

p. 547, Fig. 14 On the figure and in the caption change "aed apod" to "ej apod" and in the caption change "aedeagal apodeme" to "ejaculatory apodeme"

p. 548, col. 2 Change "Painter, R. H. 1936." to "Painter, R. H. 1938."

Chapter 42. Asilidae

p. 556, Fig. 5 Change the label and caption to "*Leptogaster (Leptogaster) cylindrica*"

p. 556, Fig. 6 Change the label and caption to "*Leptogaster (Psilonyx) annulatus*"

Chapter 45. Bombyliidae

p. 593, couplet 12*a* and 12*b* Change "R_{4+5}" to "R_5"

p. 593, couplet 13, line 1 Change "R_3" to "R_4"

Chapter 47. Empididae

p. 621, couplet 1*a* Change "*Roederiodes)*" to "*Roederioides* and *Oreogeton)*"

p. 624, col. 2, line 17 from the bottom of the page Change "191–347" to "1: 91–347"

Index

p. 644, col. 1 Delete "Apistes *17*"

p. 644, col. 2 After "Aspistes" insert "*17,*"

p. 646, col. 2 Change "Callosomae" to "callosamiae"

p. 648, col. 1 Delete "Coenomyiidae 460" and insert "460" after "*Coenomyiidae*"

p. 649, col. 1 Delete "cumeata (Townes) (Demicryptochironomus) 438"

p. 649, col. 2 Delete "Cymphomyia **505** and insert **"505"** after "Cyphomyia *502*,"

p. 650, col. 2 Change “downsi” to “downesi”

p. 651, col. 1 Change “elongate” to “elongata”

p. 651, col. 1 Insert *“594”* after “Empidideicus *97,*”

p. 651, col. 1 Insert “532” after “Empidoidea 2, 59, 68, 72,”

p. 651, col. 2 Delete “Epidieicus *594”* and “Epidoidea 532”

p. 653, col. 2 Change “Graphomyia” to “Graphomya”

p. 656, col. 2 Change “Ledomyini” to “Ledomyiini”

p. 656, col. 2 Capitalize “leptochironomus”

p. 658, col. 1 Change “Maritima” to “maritima”

p. 658, col. 2 Delete Megahyperus” and place *“18”* after “Meghyperus”

p. 658, col. 2 Capitalize “megistomastix”

p. 660, col. 1 Change *“Mycetophiloidae”* to *“Mycetophiloidea”*

p. 662, col. 2 Change “Paltostomini” to “Paltostomatini”

p. 664, col. 1 Delete “pinea (Fallén) (Neocolpodia) *262”* and insert *“262”* after “pinea (Felt) (Neocolpodia)”

p. 665, col. 2 Refer “propinqua...” to a new line

p. 666, col. 2 Delete “Pytchoptera *327”*

p. 668, col. 1 Capitalize “scythropochroa”

p. 669, col. 2 Change “Stegopogoninae” to “Stenopogoninae”

p. 671, col. 2 Insert **“455”** after “Telmatogetoninae”

p. 671, col. 2 Delete “Telomatogetoninae **455”**

p. 672, col. 1 Italicize “Tragplatte”

p. 673, col. 1 Change “unquitractor” to “unguitractor”

p. 673, col. 1 Change “vigrissal” to “vibrissal”

INDEX

This index is restricted to the taxonomic names and morphological terms associated with Diptera that appear in Volume 2 of the Manual. Similar names and terms for plants and animals other than Diptera are excluded. Bibliographic references are not indexed.

Accepted taxonomic names for all categories (suborders, infraorders, superfamilies, families, subfamilies, tribes, genera, subgenera, species, and subspecies) are given in Roman type; synonyms are in italics. Every such citation throughout the Manual is listed. Authors' names are provided for species only, followed in parentheses by the names of the genera to which the species are assigned. Subgeneric names are indexed in the same way as generic names; subspecies are indexed in the same way as species. Boldface page numbers indicate family chapters or designate where taxa appear in keys to genera; italicized numbers indicate the location of illustrations of these taxa.

The index for Volumes 1 and 2 will be incorporated in the index for Volume 3, which will have a composite index for the series.

Abapa Dodge **1174**, *1177*
Abaristophora Schmitz *690*, *693*, 694, **701**
abbreviata (Loew) (Ceriana) *724*, *727*
abdominalis (Williston) (Pseudohecamede) *1034*
aberrans (Malloch) (Earomyia) *792*
aberrans Spencer (Ophiomyia) 872
abitus Adams (Zodion) 750
abominalis (Becker) (Malloewia) 1058
abrupta (Wiedemann) (Hystricia) *1243*
Acalyptratae 917
Acanthocnema Becker *1091*, **1093**
Acanthodotheca Townsend *1172*, **1173**, *1177*
Acantholeria Garrett **979**
Acantholespesia **1211**, *1255*
Acartophthalmidae 857, **859**
Acartophthalmites Hennig 857, 861
Acartophthalmus Czerny *859*, *860*, 861
Acemya Robineau-Desvoidy **1266**
Acemyiini 1198
acerba (Walker) (Ravinia) *1170*
Acerocnema Becker *1089*, **1093**
Achaetella Malloch **1090**, *1091*
Acicephala Coquillett *1089*, **1090**
aciculata (Loew) (Cressonomyia) *1032*
Acidogona Loew **826**
Acinia Robineau-Desvoidy *823*, **829**
Aciurina Curran *823*, **828**
Acletoxenus von Frauenfeld 1012
Acontistoptera Brues *693*, *698*, *700*, *707*, **710**
Acridiophaga Townsend *1172*, **1174**, *1177*
Acridomyia Stackelberg **1100**, *1105*
acrirostris Townsend (Ginglymia) *1232*
Acroglossa Williston 1203
Acronarista Townsend 1220
Acronaristopsis Townsend 1263
Acronesia Hall *1139*, **1144**
Acrophaga Brauer & Bergenstamm 1136, *1137*, *1139*, *1141*, **1144**
Acrophagini 1135, 1136
Acroptera *679*
Acrosticta Loew *800*, 801, **806**
Acrostilpna Ringdahl *1107*, 1109, **1111**, **1112**, **1113**
Acrotaenia Loew *824*, **829**
Actenoptera Czerny *846*, 847, **851**
Actia 1239
Actia Robineau-Desvoidy *1238*, **1239**, *1241*
actinobola (Loew) (Trupanea) *823*
aculeata (Aldrich) (Acridiophaga) *1172*
acutangulus (Thomson) (Euarestoides) *824*
adamsi (Brues) (Stichillus) *690*, *693*
Adejeania Townsend 1194, *1232*, **1244**
adfinis (Cresson) (Trimerinoides) 1036
Adia Robineau-Desvoidy **1106**, **1108**
Admontia Brauer & Bergenstamm 1198, *1216*, **1228**, *1243*
adusta (Loew) (Americina) 1093
Aecothea Haliday 975, **978**
aegyptia Macquart (Eucampsipoda) 1288
aelops (Walker) (Beskia) *1229*, 1262
aenea (Fabricius) (Physiphora) *802*
aeneipes (Meijere) (Decachaetophora) *947*, *948*, 949
aeneus (Scopoli) (Eristalinus) *730*, *733*, 741
aenigma Cresson (Notiphila) *1040*
Aenigmatias Meinert 689, **696**, *697*, *705*
Aenigmatiinae **696**
Aenigmatomyia Malloch 842
aequalis (Loew) (Euaresta) *823*, *827*
aequalis Loew (Doros) 721
aequifrons (Stein) (Lispoides) *1123*, 1126
aestiva (Meigen) (Paregle) 1106
aethiops Malloch (Milichia) 908
affinis Johnson (Chaetoclusia) 857
affinis Reinhard (Paradidyma) *1209*
africanus Brauer (Pharyngobolus) 1152
Afrodinia Cogan 866
agarici (Willard) (Plesioclythia) *681*, *684*
Agathomyia Verrall 682, **683**, *684*, *685*, **686**
agens Cresson (Polytrichophora) *1031*
agilis (Meigen) (Bellardia) 1135, *1137*, *1141*, *1142*, *1143*
Agria Robineau-Desvoidy **1181**, *1183*
Agromyza Fallén *869*, 870, 871, **872**, *874*, *875*, *876*
Agromyzidae 866, **869**, 1072
agromyzina (Hendel) (Aldrichiomyza) 905, *906*
Agromyzinae 870, 871, **872**
Agromyzoidea 871
Agromyzoinea 871
alaskense Cresson (Philotelma) *1037*, 1045
Alaskophyto Townsend 1258
albibarba (Loew) (Acanthocnema) *1091*
albicans (Fallén) (Cyzenis) *1238*
albicans (Meigen) (Hecamede) *1032*, 1038
albidosa Huckett (Eremomyia) 1113
albifacies (Townsend) (Oswaldia) *1245*
albifrons (Zetterstedt) (Limnospila) *1119*, 1126
albimanus (Meigen) (Clusiodes) *855*
albipennis Meigen (Agromyza) *869*, *874*, *876*
albistylum Macquart (Ectecephala) *1053*, *1056*
albomacula Curran (Cyrtona) 1009
alcathoe (Walker) (Hylemya) *1101*
alcedo (Loew) (Chrysotachina) *1237*
alcis (Snow) (Haematobosca) 1118, *1119*
aldrichi (Curran) (Anoxynops) *1216*, 1228, *1237*
aldrichi (Malloch) (Scathophaga) *1089*
aldrichi (Mesnil) (Istocheta) *1209*, *1219*, 1224
aldrichi (Parker) (Arachnidomyia) *1159*, 1162, *1164*, *1166*, *1167*, *1170*, *1176*, *1184*
aldrichi (Townsend) (Phasia) *1217*
aldrichi Sturtevant & Wheeler (Callinapaea) *1040*
aldrichi Wheeler (Aphaniosoma) 985, *986*, 988
aldrichii Stein (Pentacricia) 1125
Aldrichina Townsend **1144**
Aldrichiomyza Hendel 903, 904, **905**, *906*
aliena Malloch (Beckerina) 702
alienum (Becker) (Oscinisoma) *1054*, 1055, *1056*
Allenanicia Townsend *1180*, **1185**
Alliopsis Schnabl & Dziedzicki **1108**
Allobosca Speiser 1273
Allognota Pokorny *1122*, **1125**
Allograpta Osten Sacken 718, **720**, **722**, *730*
Allolimosina Roháček 1004
Allomethus Hardy 748
Allometopon Kertész 854
Allomyella Malloch 1086, **1095**
Allophorocera Hendel 1198, **1215**
Allophyla Loew 975, **977**
Allopiophila Hendel *846*, 847, *848*, **852**
Allotrichoma Becker 1028, *1037*, **1038**
alma (Meigen) (Caricea) *1119*
almquisti Holmgren (Spilogona) *1123*
Alophorella Townsend 1258
alunulata Hendel (Agromyza) 870
alveofrons McAlpine (Dasiops) *792*, *793*, *794*
alypiae Sellers (Sisyropa) *1243*
amalopis group (Metasyrphus) *722*
amans (Cresson) (Neogimnomera) 1093
Amauromyza Hendel 870, 872, *874*, **877**
ambiguum (Loew) (Dictyacium) *930*
Amblycoryphenes Townsend **1173**
americana (Curran) (Bezzimyia) 1263
americana (Leach) (Icosta) *1275*, *1276*, *1278*
americana (Wiedemann) (Homoneura) *961*, *963*
americana Fitch (Meromyza) 1050, *1061*
americana McAlpine (Chaetolonchaea) *792*, 796
americana Reinhard (Dufouria) *1230*, 1262
americana Steyskal (Colobaea) 929, *930*, *931*, 937
americanum Cresson (Clanoneurum) 1033, *1040*
americanus (Wiedemann) (Eupeodes) *730*
americanus Borgmeier (Chonocephalus) *698*

americanus Peterson & Ross (Paratrichobius) *1293*, 1298
Americina Malloch **1093**, **1096**
Ametadoria Townsend *1209*, **1215**
Amiota Loew 1012, **1016**, **1017**
Amobia Robineau–Desvoidy 1161, *1179*, **1181**, *1183*
Amoebaleria Garrett *976*, *977*, **979**
amoena (Loew) (Chymomyza) *1013*
ampelus (Walker) (Panzeria) *1227*
Amphicnephes Loew **810**, *811*
Amphipogon Wahlberg 845, *846*, 847, *848*, **852**
Amputella Marshall 1004
Amygdalops Lamb 890
Anacamptomyiini 1198
Anagnota Becker 890
analis (Wulp) (Chaetogaedia) *1205*
Anaporia Townsend 1262
Anasimyia Schiner *735*, **738**
Anastomyza Malloch 992
Anastrebla Wenzel 1297
Anastrepha Schiner *820*, **821**, *822*
anaxias (Walker) (Peleteria) *1219*
anchineuria Speiser (Ornithomya) *1271*, *1276*, *1279*
Androeuryops Beneway 1198
Anevrina Lioy *693*, **696**, *697*, *699*
Angioneura Brauer & Bergenstamm 1136, *1139*, **1140**, *1141*, 1189, 1200
Angioneurinae 1135
Angioneurini 1134, 1135, 1136, **1140**
angulata (Thomson) (Poecilosomella) 994, *996*, *998*, 1000
angulatus Wirth (Canaceoides) 1080
angustata (Wulp) (Hyphantrophaga) 1207
angustata Coquillett (Stenomicra) *893*
Angustia Sellers **1225**
angustifrons Rondani (Cirillia) 1189
angustipennis (Loew) (Tephritis) *817*
angustipennis Melander (Strongylophthalmyia) *777*, *779*
angustivitta (Aldrich & Webber) (Angustia) 1225
Anicia Robineau–Desvoidy *1180*, *1183*, **1185**
anilis Fallén (Dryomyza) *923*, 924, *925*
Anisia Wulp 1198, **1233**, **1266**
annectans Sturtevant (Periscelis) 898
annulata (Fallén) (Periscelis) *895*, *896*, *897*
annulicornis (Malloch) (Mesosphaerocera) *997*, 1004
annulipes (Meigen) (Enicita) *947*
annulipes Loew (Periscelis) 897
annulus (Walker) (Crumomyia) *997*, *998*
Anolisimyia Dodge 1162, 1174$
anomala (Cole) (Coelopina) 922
Anomalochaeta Frey 882, *883*, **884**
Anorostoma Loew 975, *976*, **978**
Anoxynops Townsend *1216*, **1228**, *1237*
antennaepes (Say) (Rainieria) *762*, *764*, 765, *766*, 767
antennalis (Coquillett) (Chaetocrania) 1203, *1204*
antennalis (Reinhard) (Drino) *1240*
antennalis Townsend (Phasmophaga) *1231*
antennata (Rondani) (Erynniopsis) 1233
Anthomyia Meigen *1099*, **1102**, *1107*
Anthomyiella Malloch **1106**, *1107*
Anthomyiidae 924, 1087, **1099**, 1116, 1189
Anthomyiinae **1102**
Anthomyiini **1102**
Anthomyiopsis Townsend *1232*, **1265**
Anthomyza Fallén *887*, *888*, **890**
Anthomyzidae 882, **887**, 892
Anthomyzoidea 782, 882, 898, 1075
anthracina (Czerny) (Lasiomma) *1103*, *1104*
anthracinus (Bigot) (Oxynops) 1228
Anthracomyia Rondani 1188
Anthracophaga Loew **1066**
Anticheta Haliday 927, 928, 929, **931**, *935*, **937**
antiqua (Meigen) (Delia) *1103*
antitheus Walker (Chrysogaster) *724*
antrozoi (Townsend) (Basilia) *1284*
anus (Meigen) (Curtonotum) 1009
anxia (Zetterstedt) (Hydrotaea) *1120*, *1123*
Anypotacta Czerny **979**
Anzamyia Reinhard 1250
Apachemyia Townsend 1264
Apallates Sabrosky **1052**, **1060**, *1061*
Apetaenus Eaton 1074, 1075
Aphaniosoma Becker 985, *986*, 987, **988**
Aphanotrigonum Duda *1053*, *1057*, **1063**
Aphantorhapha Townsend 1239
Apheloglutus Greene 1220
Aphiochaeta Brues **706**
Aphria Robineau–Desvoidy *1231*, **1264**
Aphriini 1194, 1264
apicalis (Meigen) (Geomyza) *883*
apicalis (Williston) (Acrosticta) *800*
apicalis Curtis (Scathophaga) *1088*
apicalis Dalman (Diopsis) 788
apicalis Loew (Chyliza) *783*
apicifer (Walker) (Archytas) *1231*
Apinops Coquillett 1258
Apis 751
Aplomya 1207, 1212
Aplomya Robineau–Desvoidy 1196, 1197, 1201, **1211**, 1212
Aplomyopsis Townsend **1212**
Apocephalus Coquillett *691*, **703**, *705*
Apophoneura Malloch 992
Apostrophus Loew 1258
Apotropina Hendel 1049, **1051**
Appendicia Stein 1261
appendicula group (Limosina) 1003
approximatonervis (Zetterstedt) (Pseudopachychaeta) *1054*, 1065
Apteromyia Vimmer **999**, 1003
Aptilotus Mik **995**, *1001*, **1003**
aquila (Fallén) (Parydra) *1035*
Arabiopsis Townsend *1180*, **1182**
Arachnidomyia Townsend *1159*, 1162, *1164*, *1166*, *1167*, **1168**, *1170*, *1176*, *1184*
Aralia 758
aranea (Coquillett) (Megistopoda) 1296, 1297
Aravaipa Townsend 1203
Archiborborus Duda 994
Archimimus Reinhard *1165*, **1174**
archippivora (Riley) (Lespesia) *1237*
Archytas Jaennicke *1231*, **1244**
arctica (Holmgren) (Arctopiophila) *851*
arctica (Malloch) (Borborillus) *998*
arctica (Sack) (Trafoia) *1230*, 1262
arctii Spencer (Liriomyza) *876*
Arctophila Schiner 729, **738**
Arctophyto Townsend *1223*, **1248**
Arctopiophila Duda *848*, *851*, **852**
Arctosyrphus Frey *726*, **741**
arcuata (Loew) (Euthycera) *930*, 934, *935*, 938
arcuatus (Say) (Xanthomelanodes) *1243*
ardeae (Macquart) (Icosta) 1274
argentata (Walker) (Brachydeutera) *1031*
argentifrons Coquillett (Pseudochaeta) *1208*
Argoravinia Townsend **1163**
argus (Zetterstedt) (Ernoneura) 1087, *1091*
argyrocephala (Meigen) (Metopia) *1180*
arida Reinhard (Psilopleura) *1231*, 1251
aristalis (Coquillett) (Sciomyza) 928, *930*
aristalis (Coquillett) (Oebalia) *1179*, 1182, *1183*
aristalis Townsend (Ostracophyto) *1227*, 1261
arizonicus Wheeler (Paraneossos) 978
armigera (Coquillett) (Eucelatoria) *1238*
arnaudi Borgmeier (Neodohrniphora) *691*, *697*, 702
arnaudi Wirth (Nocticanace) *1081*
arpidia (Malloch) (Psilacrum) 1055
Ascodipteridae 1297
Ascodipterinae 1294, 1295, 1297
Ascodipterinae 1297
Ascodipteron Adensamer 1295, 1296

Asemosyrphus Bigot *726*, **738**
Asiconops Chen **753**
Asilidae 904
Asiosphegina Stackelberg **732**, *733*
Asmeringa Becker 1027, **1038**
Asseclamyia Reinhard *1205*, **1214**
assimilis (Townsend) (Oswaldia) *1243*
Asteia Meigen *899*, 900, **902**
Asteiidae 898, **899**, 917, 966
Astiosoma Duda 899, **900**, *901*
Atacta Schiner *1208*, **1215**
Atactopsis Townsend *1205*, **1214**, *1235*
Atelestus Walker 683
Ateloglossa Coquillett 1248
ater Meigen (Pipunculus) *745*
Athanatus Reinhard 1254
Atherigona Rondani *1119*, **1125**
Athrycia Robineau – Desvoidy *1219*, **1250**
Athyroglossa Loew 1028, *1031*, **1033**
Atissa Haliday *1034*, **1038**
atlanis (Aldrich) (Blaesoxipha) *1172*, 1173
atra (Meigen) (Lotophila) 1004
atra Malloch (Macateeia) 1112
atramentaria (Meigen) (Stevenia) 1188, 1189
atrata (Coquillett) (Opesia) *1217*, 1265
atratula Ratzeburg (Leucopis) 966
Atriata *679*
atricauda (Zetterstedt) (Acrostilpna) *1107*
atriceps (Zetterstedt) (Boreellus) *1137*, *1139*, 1140, *1142*
Atrichomelina Cresson 927, **929**, *935*, *936*, **937**
atricornis (Meigen) (Allophyla) 977
atrifacies Aldrich (Leucopis) *970*
atrifrons (Coquillett) (Neochirosia) *1089*, *1092*
atripennis Coquillett (Chaetoplagia) *1241*, 1250
atriventris (Walker) (Diotrephes) 1206, *1245*
Atrophopalpus Townsend 1218
atrophopodoides Townsend (Vanderwulpia) *1229*
aucta (Fallén) (Verrallia) *747*
auditrix Shewell (Colcondamyia) *1164*
Aulacigaster Macquart *891*, **892**, *893*
Aulacigastridae 890, **891**, 898
aurata (Coquillett) (Macronychia) *1179*
aurata Robineau – Desvoidy (Hemyda) *1217*, 1259
aurea (Macquart) (Lamprolonchaea) *795*, 796
australis (Hutton) (Macrocanace) 1075
australis D.K. McAlpine (Cypselosoma) 758
Austrophorocera Townsend **1221**
Automola Loew **834**, *835*, *836*
autumnalis (Townsend) (Distichona) *1204*
Auxanommatidia Borgmeier *692*, *693*, *698*, **703**
Axinota Wulp 1007, 1009
Axiologina Hendel **806**
Axysta Haliday **1043**
Azelia Robineau – Desvoidy *1119*, **1124**
Baccha Fabricius *714*, *719*, 720, **721**
Bactropalpus Borgmeier *693*, *709*, **710**
badia (Walker) (Blera) *735*
Baeomyia O'Hara **1236**
Baeopterus Lamb 922
bahamensis Wirth (Paraglenanthe) 1039
Bahamia Sabrosky **900**
bakeri Coquillett (Chaetoclusia) *855*
balachowskyi Mesnil (Geomyza) *883*
barbata (Coquillett) (Medina) *1217*, *1252*
barbata (Zetterstedt) (Pogonota) 1087, *1088*, *1092*
barbata Loew (Xylota) *726*
Basilia Ribeiro *1283*, *1284*, 1287, 1288, 1289
batesi (Curran) (Neosilba) *792*, *793*
bathybothyra Speiser (Basilia) 1289
Batrachomyia Krefft 1050
beameri Steyskal (Xenopterella) *957*, 964
beata Aldrich (Asteia) *899*
Bebryx Gistel 1118
Beckerina Malloch *691*, *700*, **702**
Beckerinini 695, **702**
Beebeomyia Curran 834
Belida Robineau – Desvoidy 1197, 1201, 1233, *1234*, **1236**
bella (Williston) (Cynorhinella) *725*
Bellardia Robineau – Desvoidy 1134, 1135, *1137*, *1141*, *1142*, *1143*, **1144**
Bellieria Robineau – Desvoidy *1164*, **1169**, *1171*
Bellieriini **1169**
Belvosia Robineau – Desvoidy **1214**
benefica Malloch (Pseudoleucopis) 967
Bengalia Robineau – Desvoidy 1135
Bercaea Robineau – Desvoidy 1162, **1169**, *1171*, *1176*
Bercaeopsis Townsend **1168**
bergi Cresson (Hydrellia) *1044*
bermudensis Parsons (Conops) 753
berryi Cockerell (Drosophila) 1012
Bertamyia Kessel 682, **683**, *684*, **686**, *687*
Beskia Brauer & Bergenstamm *1229*, **1262**
Bessa Robineau – Desvoidy 1199, 1200, **1221**
Besseria Robineau – Desvoidy *1252*, **1258**, **1262**, **1263**
betulae Sabrosky (Odinia) *863*
Bezzimyia Townsend 1193, 1195, 1200, *1229*, **1263**
biannulata (Say) (Stylogaster) *755*
bicolor (Williston) (Xanthoepalpus) 1244, *1246*
bicolor (Zetterstedt) (Eurygnathomyia) 840
bicolor Loew (Sigaloessa) *901*
bicolor Oldenberg (Acartophthalmus) 861
bifrons (Stenhammar) (Spelobia) 999
Bifronsis Roháček **999**
bigeloviae (Cockerell) (Aciurina) *823*
bigelowi (Curran) (Cleonice) *1230*, *1238*
Bigotomyia Malloch 1118
bilinearis (Williston) (Lejops) *735*
Billaea Robineau – Desvoidy 1198, 1200, *1223*, **1248**
biloba Clausen (Pelina) *1037*
bimarginipennis Karsch (Physocephala) *755*
binotata (Cresson) (Hyadina) *1035*
Biorbitella Sabrosky **1058**, 1064
bipunctatus (Fallén) (Mycetaulus) *850*
bipustulata Wulp (Xanthacrona) 807
bisetosa (Coquillett) (Paracoenia) *1040*, *1042*
bishoppi (Sabrosky) (Liohippelates) *1061*
bispina (Loew) (Homoneura) *957*, *960*
bispinosa (Coquillett) (Paracoenia) 1029
Bithoracochaeta Stein **1125**
Blaesoxipha Loew *1172*, **1173**
blakeae Dodge (Anolisimyia) 1174
blanda (Osten Sacken) (Hyphantrophaga) *1252*
Blepharipa Rondani **1213**, *1243*, *1252*
Blepharomyia Townsend *1226*, **1258**
Blera Billberg *735*, **736**, **737**
Blondelia Robineau – Desvoidy **1224**, *1245*
Blondeliini 1194, 1195, 1196, 1197 1198, 1201, 1221
Bocainamyia Albuquerque *846*
Boettcheria Parker *1166*, *1167*, **1174**, *1175*, *1184*
Boettcheriina 1162
Boettcheriini **1174**
Bolomyia Brauer & Bergenstamm 1210
bomboides Hunter (Pocota) 736
bombylans (Linnaeus) (Volucella) *728*, 737, *740*
Bombyliomyia Brauer & Bergenstamm **1202**, *1245*
Bombyliopsis Townsend 1202
Bonnetia Robineau – Desvoidy 1257
Borborillus Duda 994, *998*, **1004**
Borboropsidae 975
Borboropsis Czerny 974 975, *976*, **978**
borealis Brues (Mesophora) 703
borealis Curran (Lonchoptera) 679
borealis Czerny (Trichochlamys) 979
borealis Shewell (Camptoprosopella) *956*, *959*
Boreellini 1135
Boreellus Aldrich & Shannon 1134, *1137*, *1139*, *1142*, **1140**
Boreopiophila Frey 845, **852**

Boreothrinax Steyskal 813, **814**, *815*
Borophaga Enderlein *690*, **701**
borrichia Bush & Huettel (Cecidocharella) 825
bostoni McAlpine & Martin (Sciadophora) 695
Botanophila Lioy 1099, 1102, *1105*, **1109**, *1110*, **1112**, **1114**
bovis (Linnaeus) (Hypoderma) 1150, *1153*, *1154*
Brachicoma Rondani 1161, **1178**, *1179*, *1184*
Brachycera 679
Brachydeutera Loew **1030**, *1031*
Brachyopa Meigen *728*, **732**, **737**, *740*
Brachypalpus Macquart *725*, *726*, **736**
brachyrhynchus (Macquart) (Physoconops) *749*
Brachytarsina Macquart 1295, 1297
brasiliensis Schiner (Atacta) *1208*
brasiliensis Schmitz (Acontistoptera) *707*
Braula Nitzch *913*, *915*, 916, 917
Braulidae **913**
Braulomorpha 917
breviata (Meunier) (Prosphyracephala) 789
brevicornis (Say) (Sphyracephala) *785*, *787*, 788, 789
brevicostata (Duda) (Spinilimosina) 1003
brevipennis (Loew) (Besseria) *1252*
brevis (Cresson) (Renocera) *930*
brevis Coquillett (Paradmontia) *1222*
brevis Huckett (Proboscimyia) *1104*
brimleyi Sabrosky (Rhodesiella) 1055, *1057*
Bromeloecia Spuler **999**
Brontaea Kowarz 1118, *1123*, **1130**
Brooksiella Vockeroth **1094**
brumalis Czerny (Oldenbergiella) 978
brunnea (Brooks) (Graphogaster) *1240*
buccata (Fallén) (Heterocheila) 924
buccata (Fallén) (Oedoparea) 926
buccata (Linnaeus) (Myopa) *755*
Bucephalina Malloch **1093**
Bucephalomyia Malloch 1118
Bufolucilia Townsend 1135, **1144**
bullata (Parker) (Neobellieria) 1161, *1176*
Buquetia Robineau–Desvoidy **1214**
buresi Cresson (Ephydra) 1029
bysia (Walker) (Phaonia) *1120*, *1123*
Cacozelus Reinhard 1257
cadaverina Robineau–Desvoidy (Cynomya) *1137*, *1139*, *1143*
Cadrema Walker 679, **1051**, *1056*, *1059*, *1061*
caecus Edwards (Trichobius) 1296, 1297, *1299*
caerulescens Hendel (Setellida) 833, 834
caerulescens Loew (Senopterina) *811*
caesar (Aldrich) (Eumea) 1212
Cairnsimyia Malloch 989, 990, 992
Calamoncosis Enderlein *1053*, **1055**
calcitrans (Linnaeus) (Stomoxys) 1118
californica (Coquillett) (Valentibulla) *823*
californica Borgmeier (Auxanommatidia) *692*, *698*, 703
californica Kessel (Protoclythia) 686
californicum Smith (Spilochaetosoma) *1227*, 1261
californicus (Coquillett) (Meledonus) 1254
calla Kessel (Callomyia) *684*
Callachna Aldrich **824**
Callicera Panzer *719*, **723**
Callinapaea Sturtevant & Wheeler 1030, *1040*, **1041**
Calliopum Strand **954**, *959*, *961*
Calliphora Robineau–Desvoidy *1133*, 1135, *1137*, *1138*, *1139*, *1142*, **1144**
Calliphoridae **1133**, 1160, 1161, 1162, 1188, 1189, 1195, 1200
Calliphorinae **1136**
Calliphorini 1135, 1136, **1140**
Callomyia Meigen 682, **683**, *684*, **686**, *687*
Callopistromyia Hendel **807**
Calobata Meigen 763
Calobatidae *763*
Calobatina Enderlein **765**, **767**
Calobatinae 761, **763**
Calocoenia Mathis *1037*, **1045**
Calodexia Wulp 1198
Calolydella Townsend 1197, **1236**
Calotarsa Townsend 682, *684*, *685*, **686**, *687*, **688**
Calycomyza Hendel *874*, **877**
Calyptratae 897, 1187
Calythea Schnabl & Dziedzicki **1106**
camatus Reinhard (Archimimus) *1165*, 1174
Camelomyia Reinhard 1224
Camilla Haliday *1023*, *1024*, 1025
Camillidae 1009, **1023**, 1030
Campanulomyza Nowakowski 872
campestris (Fallén) (Anicia) *1180*, *1183*
Campichoeta Macquart 1020, **1022**
Campichoetidae 1022
Campichoetidae 1030
Camptoprosopella Hendel **954**, *956*, *959*
Camptops Aldrich *1166*, **1178**
Campylochaeta Robineau–Desvoidy *1229*, **1260**
Canace 1080
Canacea Cresson *1079*, **1080**, *1081*, *1082*, **1083**
Canaceoides Cresson 1080, *1081*, **1082**, **1083**
Canacidae 1075, **1079**
canadambra McAlpine & Martin (Prioriphora) 695
canadensis (Brooks) (Gymnosoma) *1223*
canadensis (Johnson) (Herina) *800*
canadensis (Loew) (Epochra) 826
canadensis (Macquart) (Trypetoptera) 934
canadensis Hardy (Dorylomorpha) *747*
canadensis Johnson (Agathomyia) *684*, *685*
canadensis Snyder (Acridomyia) *1105*
canadensis Snyder (Lispe) *1119*
canariensis (Macquart) (Pseudolynchia) 1274, *1276*, *1278*
canicularis (Linnaeus) (Fannia) *1122*, *1129*
capillata (Loew) (Clinoceroides) 1093
capillata Loew (Cheilosia) *726*
capitata (Wiedemann) (Ceratitis) 818, *822*, 825
capitata Townsend (Cockerelliana) *1222*, 1251
capito Loew (Oedopa) *800*
carbonaria (Kessel) (Grossovena) *685*, 686
carbonarium (Loew) (Rhopalopterum) *1056*
Carcelia Robineau–Desvoidy *1204*, **1210**, *1243*
Caricea Robineau–Desvoidy 1118, *1119*, **1125**
Carinosillus Reinhard 1248
Carnidae **909**, 917, 1072
Carnus Nitzsch *909*, *910*, **910**
carolae Capelle (Rhopalosyrphus) 729
carpenteri Hennig (Succinasteia) 900
Cartosyrphus Bigot *731*
casei (Linnaeus) (Piophila) *845*, 847, 852
cata (Melander & Brues) (Pericyclocera) 704
Cataclinusa Schmitz *693*, *698*, **708**
Catalinovoria Townsend 1250
Catalpomyza Spencer 872
Catemophrys Townsend 1260
Catharosia Rondani *1242*, **1259**
Cattasoma Reinhard **1181**
caudata Fallén (Notiphila) 1028, 1029, *1035*
caudata group (Notiphila) 1029, 1039
cauta (Townsend) (Hypovoria) *1219*
cavernicola Papp (Katacamilla) 1025
cavicola Townsend (Chiricahuia) 1257
Cecidocharella Hendel **825**
Cecidomyiidae 795
Celatoria Coquillett *1216*, **1228**, *1255*
celeris (Townsend) (Neomintho) *1238*
Cenosoma Wulp 1260
Centrioncus Speiser 785
Cephalia Meigen **801**
Cephaloglypta 1199
Cephalomyza 877
Cephalopina Strand 1156
Cephalops Fallén **748**
Cephalosphera Enderlein **748**
Cephalosphera Enderlein 746

Cephenemyia Latreille 1148, 1149, 1152, *1153*, **1156**, **1157**
Cephenemyiinae 1152
Cephodapedon Malloch 982, 987
Ceracia Rondani **1218**, *1231*
Ceranthia Robineau–Desvoidy **1239**, *1241*
Ceratinostoma Meade **1090**
Ceratitis Macleay 818, 821, *822*, **825**
Ceratobarys Coquillett **1051**, *1059*
Ceratomyiella Townsend 1218
cerea (Coquillett) (Gimnomera) *1089*
Ceriana Rafinesque *724*, *727*, **729**
Cerioides Rondani 723
Cerioidini 717, 718
Cerodontha Rondani 870, *873*, **877**
Ceromasia Rondani *1217*, **1218**
Ceromya Robineau–Desvoidy **1239**
Ceropsilopa Cresson *1032*, **1036**
Ceroptera Macquart 994, **1000**, *1001*
Ceroxys Macquart *799*, *802*, **808**
certimus Adams (Chlorops) *1049*, *1056*, *1057*, *1059*
cervi (Linnaeus) (Lipoptena) 1274
Cetema Hendel *1061*, **1065**
Chaetexorista Brauer & Bergenstamm **1221**
chaetifrons Steyskal (Texasa) 805
Chaetoapnaea Hendel *1035*, *1040*, **1041**
Chaetochlorops Malloch 1051, **1052**, *1061*
Chaetoclusia Coquillett *855*, **857**, 861
Chaetoclusiella Soós 861
Chaetocrania Townsend **1203**, *1204*
Chaetogaedia Brauer & Bergenstamm *1205*, **1214**
Chaetoglossa Townsend *1208*, **1213**, *1234*
Chaetolonchaea Czerny *792*, 795, **796**
Chaetonodexodes Townsend **1228**, **1239**, *1245*
Chaetonopsis Townsend *1238*, **1265**
Chaetophlepsis 1260
Chaetoplagia Coquillett 1195, *1241*, **1250**
Chaetopleurophora Schmitz **696**, *709*
Chaetopsis Loew *800*, *802*, **806**
Chaetosa Coquillett *1089*, **1095**
Chaetostigmoptera Townsend 1220, **1233**, *1240*
Chaetostomella Hendel *818*, **825**
Chaetovoria Villeneuve *1222*, **1251**
chagnoni (Johnson) (Pyrgotella) 814, *815*
Chalarinae 745, **746**
Chalarus Walker 746, *747*, **748**
Chalcosyrphus Curran 718, *725*, *733*, **734**
Chamaemyia Meigen *965*, **967**
Chamaemyiidae 897, 917, **965**, 1072
Chamaemyiinae 966, **967**
Chamaemyiini **967**
Chamaesyrphus Mik *724*, **731**
Cheilosia Meigen 716, 717, 718, *724*, *726*, **731**, **732**
Chelisia Rondani 1099, **1102**, *1105*
Chelisiini **1102**
chelonei Spencer (Phytomyza) *876*
Chesippus Reinhard **1206**
Chetogena Rondani *1209*, **1221**, *1240*
Chetostoma Rondani **825**
Chiastocheta Pokorny **1102**, *1103*
Chilomyia Shannon 731
Chiricahuia Townsend *1242*, **1257**
Chironomidae 1029
Chirosia Rondani **1102**
Chlorohystricia Townsend **1202**, *1245*
Chloropidae 679, 840, 900, 904, 917, **1049**, 1070, 1072, 1075
Chloropinae 1050, **1051**
Chloroprocta Wulp **1136**, *1139*
Chlorops Meigen *1049*, 1050, *1056*, *1057*, *1059*, *1062*, **1066**
Cholomyia Bigot **1265**
Chonocephalus Wandolleck *693*, *698*, *707*, **708**, **711**
Chromatocera Townsend 1220
Chromatomyia Hardy 872, **878**
Chrysagria Townsend **1163**, *1167*
Chrysoexorista Townsend *1204*, **1206**
Chrysogaster Meigen 716, 717, *724*, **731**, **732**
Chrysomya Robineau–Desvoidy 1135, 1136
Chrysomyiinae **1136**
Chrysomyiini 1135, **1136**
Chrysomyza Fallén 806
Chrysosomidia Curran **736**
Chrysotachina Brauer & Bergenstamm 1200, **1202**, *1237*
Chrysotoxum Meigen 715, **718**, *719*, *735*
Chyliza Fallén **782**, *783*
Chylizinae **782**
Chymomyza Czerny *1013*, *1015*, **1017**
Chyromya Robineau–Desvoidy *985*, *986*, **987**
Chyromyidae **985**
cilipes (Haliday) (Azelia) *1119*
cimbicis (Townsend) (Boettcheria) *1184*
cimiciforme Loew (Notogramma) *802*
cincta (Loew) (Spaziphora) 1095
cincta Townsend (Miamimyia) 1239
cinctella (Zetterstedt) (Meliscaeva) 720, *730*
Cinderella Steyskal 975, **978**
cineracea (Coquillett) (Neodeceia) *955*, 958
cinerea (Coquillett) (Athrycia) *1219*, 1250
cinerea (Loew) (Olcella) *1054*, *1061*
cinerea (Townsend) (Estheria) *1219*, *1241*, 1247
cinerea Jones (Ephydra) 1028, 1029, 1044
cinerea Townsend (Meigenielloides) 1233
cinereiventris (Zetterstedt) (Lophosceles) *1120*
cingarus (Aldrich) (Oxysarcodexia) *1164*, *1167*
Cinochira Zetterstedt 1259, **1263**
Circia Malloch **1102**
Cirillia Rondani 1188, 1189
Cirrula Cresson 1028, 1029, *1037*, **1044**
Cistogaster Latreille 1259
cistudinis (Aldrich) (Cistudinomyia) 1163
Cistudinomyia Townsend 1161, **1163**
Citrago Schmitz *691*, 696, **701**
citreifrons (Malloch) (Mallochomyza) *959*, *961*, 963
Cladochaeta Coquillett 1012, **1016**, **1017**
Clairvillia Robineau–Desvoidy 1259, **1263**
Clanoneurum Becker 1029, **1033**, *1040*
claripennis (Reinhard) (Gymnophryxe) *1208*, 1214
claripennis Malloch (Palloptera) 842
Clasiopella Hendel 1028, *1032*, **1036**
Clastoneuriopsis Reinhard **1221**, *1230*, **1260**
claterna Reinhard (Impeccantia) *1231*, 1266
clathrata (Loew) (Paroxyna) *824*
clausa Brauer & Bergenstamm (Oestrophasia) *1217*, *1242*
Clausicella Rondani *1229*, *1234*, **1264**
clavatus (Fabricius) (Pseudodoros) *719*, 721
clavipes (Fabricius) (Ropalomera) 942
claytonae Wheeler & Takada (Mycodrosophila) *1013*
Clemelis Robineau–Desvoidy *1208*, 1210, **1211**
clemonsi Townsend (Spathidexia) *1252*
Cleonice Robineau–Desvoidy 1195, 1201, *1230*, *1238*, **1262**
Clinoceroides Hendel **1093**
clistoides (Townsend) (Gnadochaeta) *1226*
Clistomorpha 1260
Clistomorpha Townsend 1260
Cloacina Reinhard **1214**
clunipes (Meigen) (Spelobia) 994, *997*, *1001*
Clusia Haliday *853*, *855*, *856*, **857**
Clusiidae **853**, 861, 866, 871
Clusiinae **857**
Clusiodes Coquillett 853, 854, *855*, **857**
Clusiodinae **857**
Cnemodon Egger *731*
Cnodacophora Czerny *762*, *764*, **765**
Cobboldia Brauer 1150
coccidella Townsend (Eumasicera) *1232*, *1256*
cocciphila (Coquillett) (Syneura) *692*, *698*, 704
Cochisemyia Reinhard 1254
Cochliomyia Townsend 1135, **1136**, *1137*, *1139*

Cochliomyiini 1135
cockerellae (Aldrich) (Pierretia) 1169, *1171*
Cockerelliana Townsend *1222*, **1251**
cocklei Townsend (Arabiopsis) *1180*, 1182
coeca Nitzsch (Braula) *913*, *915*, 916, 917
Coelomyia Haliday 1118
Coelomyia Haliday 1124
Coelopa Meigen *919*, 920, *921*, **922**
Coelopella Malloch 922
Coelopidae **919**, 1075
Coelopina Malloch 919, 920, **922**
Coenia Robineau-Desvoidy **1045**
Coenosia Meigen 1116, 1118, *1120*, *1123*, **1125**, **1126**
Coenosiinae 1116, 1117
Coenosopsia Malloch 1100, **1102**
Colcondamyia Reinhard 1161, **1163**, *1164*
Coleophasia Townsend 1250
coleoptrata (Scopoli) (Stegana) *1013*
collaris Loew (Psila) *781*, *783*
Collinella Duda 997
collini Carpenter & Hull (Protonephrocerus) 746
Colobaea Zetterstedt 927, 928, **929**, *930*, *931*, **937**
coloradense Garrett (Anorostoma) *976*
coloradensis (Aldrich) (Servaisia) *1184*
Coloradomyia Arnaud **1257**
colorata Walker (Drosophila) *1013*
comans Sabrosky (Pholeomyia) 904
Comasarcophaga Hall 1160, *1165*, **1168**, *1170*, *1177*
Comasarcophagini **1163**
comma (Wiedemann) (Eurosta) *822*
Commoptera Brues *698*, *707*, **710**
compressiceps Borgmeier (Lecanocerus) *691*, *697*, 703
Compsilura Bouché **1224**
Compsobata Czerny *762*, *764*, **765**, *766*
comstocki (Williston) (Acantholespesia) 1211
comstocki Townsend (Eulasiona) *1209*
concinnata (Meigen) (Compsilura) 1224
concolor (Malloch) (Gymnochiromyia) *986*
condecens Reinhard (Erynnia) *1205*
confluens Loew (Hydromyza) *1089*, 1093
confusa Aldrich (Masiphya) *1232*
conica (Malloch) (Rhyncophoromyia) *692*
Coniceps Loew 833, *835*, **836**
Conicera Meigen *690*, *693*, *697*, *699*, **701**, **702**, *709*
Coniceromyia Borgmeier *690*, *699*, **701**
conicola (Greene) (Hapleginella) *1053*, *1057*, 1060
Conioscinella Duda **1051**, **1064**
Conopidae **749**, 751
Conopinae 749, 750, **751**, **756**
Conopini 749, **751**
Conops **753**, **754**
consobrina Zetterstedt (Platypeza) *685*
constrictor (Malloch) (Paraprosalpia) *1107*, *1110*
cooleyi (Seamans) (Lejops) *726*, 741
Copecrypta Townsend *1219*, **1239**
Copestylum Macquart 716, 717, 718, **737**
Coproica Rondani **995**, *996*, *998*
Copromyza Fallén *996*, *998*, **1004**
Copromyzinae 994, **995**
coquilletti (Aldrich) (Cyrtophleba) *1222*
coquilletti (Hendel) (Physoclypeus) *955*, 958
coquilletti (Williston) (Dideomima) 723, *727*
coquilletti Cresson (Ceropsilopa) *1032*
coraxa (Kessel) (Paraplatypeza) *685*
Cordilura Fallén 1086, 1087, *1088*, *1089*, **1090**, *1091*, *1092*
Cordilurina James **1090**, *1091*, *1092*
Cordyligaster Macquart **1249**
Cordylurella Malloch **1095**
cornicina (Fabricius) (Neomyia) 1121, *1122*
cornuale Reinhard (Crocinosoma) *1229*, 1265
cornuta (Bigot) (Dohrniphora) *690*, *697*, *699*, *709*
coronata (Loew) (Pelomyia) *1076*, *1077*
Coronimyia Townsend 1264
corrigiolata Linnaeus (Micropeza) 763
corticalis (Loew) (Pseudotephritis) *804*
corticis group 796
corticis Taylor (Lonchaea) *794*
corvina Malloch (Paraleucopis) *968*, *969*
corynorhini (Ferris) (Basilia) *1284*
corynorhini Cockerell (Trichobius) *1293*, 1297
Cosmetopus Becker *1091*, **1094**
costalis (Curran) (Xeniconeura) *955*, *957*, 958
costata (Loew) (Elachiptera) *1056*, *1059*
cothurnatus Bigot (Microdon) *727*, *733*
coxata (Stenhammar) (Leptocera) *998*
coxata Ferris (Nycterophilia) *1299*
coxendix (Fitch) (Apallates) *1061*
coylesi Spencer (Phytobia) 877
Craspedochoeta Macquart **1109**, **1112**
crassata Garrett (Pseudoleria) 975
crassimana group (Limosina) 1003
crassinervis (Walton) (Chaetostigmoptera) *1240*
crassipalpis (Macquart) (Liopygia) *1176*
crassiseta (Aldrich & Webber) (Prooppia) 1207
crassispinosa Wood (Policheta) *1217*
Cremersia Schmitz *697*, *700*, **703**, *709*
Cremifania Czerny **966**
Cremifaniinae **966**
Cressonomyia Arnaud *1032*, **1036**
cribellum (Loew) (Pseudotephritina) *802*
cribrata (Stenhammar) (Scatophila) *1040*
criddlei Curran (Cordilura) *1088*
Crinophleba Borgmeier *690*, **696**, *699*
Crinurina Karl **1106**
Crioprora Osten Sacken *725*, **736**
Criorhina Meigen **736**
crocata Reinhard (Macromya) 1202, *1234*
Crocinosoma Reinhard *1229*, **1265**
Crumomyia Macquart 995, *997*, *998*, **1004**
Cryptochetidae **1069**
Cryptochetum Rondani *1069*, *1070*, 1072
Cryptomeigenia Brauer & Bergenstamm 1198, *1209*, **1225**
Cryptotreta Blanc & Foote **829**
Cucullomyia Roback **1169**
culta (Wiedemann) (Paracantha) *823*
Cuphocera 1239
currani Kessel (Metaclythia) 683, *684*
Curranops Harriot 801, **805**
Curtonotidae **1007**, 1025, 1030
Curtonotum Macquart *1007*, *1008*, 1009
curvicauda Gerstacker (Toxotrypana) 821, *822*
curvipes (Wiedemann) (Lejops) *733*, *735*, 738
curvipes Latreille (Sphaerocera) *993*, *996*, *997*, *998*, *1002*
Cuterebra Clark *1147*, 1148, 1149, 1150, *1153*, *1155*, **1156**, **1157**, 1199
Cuterebrinae 1149, 1150, 1152, 1189
cuthbertsoni Duda (Curtonotum) 1009
Cyamops Melander **892**, *893*
cyaneiventris (Wulp) (Chlorohystricia) 1202, *1245*
Cyanus Hall **1144**
Cyclopodia Kolenati 1283, 1285
Cyclopodiinae 1289
Cyclorrhapha 679
cyclorrhaphous Brachycera 679
cylindrica (Stein) (Eutrichota) *1104*
cylindrica Say (Loxocera) *783*
Cylindromyia Meigen 1196, **1259**
Cynomya Robineau-Desvoidy 1134, *1137*, *1139*, *1143*, **1144**
Cynorhinella Curran *725*, *727*, **732**, *733*, **734**, **737**
cypseloides Townsend (Anthomyiopsis) *1232*, 1265
Cypselosoma Hendel 758, 760
Cypselosomatidae **757**
Cypselosomatinae 757, 758, 760
Cypselosomatites Hennig 760
Cyrtona Séguy 1009
Cyrtoneurina Macquart 1117
Cyrtoneurininae 1117

Cyrtonotinae 1009
Cyrtophleba Rondani *1222*, **1250**
Cyzenis Robineau-Desvoidy **1210**, *1238*
Dacinae **821**
dacotensis Townsend (Euscopolia) *1222*
Dacus Fabricius **821**, *822*
daeckei Johnson (Nephrocerus) *747*
Dahlimosina Roháček **1002**
dakotensis Townsend (Euscopolia) 1251
Dalmannia Robineau-Desvoidy 750, 751, *752*, *753*, **754**, *755*, **756**
Dalmanniinae 749, 750, 751, **754**, **756**
Dasiopinae **795**
Dasiops Rondani *792*, *793*, *794*, **795**
Dasyopa Malloch *1054*, **1064**
dasyprocta (Loew) (Okeniella) *1092*, 1094
Dasyrhicnoessa Hendel 1075
Dasysyrphus Enderlein **722**
dauci (Meigen) (Conicera) *690*, *693*, 702
davisii (Walton) (Phytomyza) 878
debile (Townsend) (Pseudopachystylum) *1252*, 1257
debilis Loew (Elliponeura) *1057*
debilis Loew (Philygria) *1035*
Decachaetophora Duda *947*, *948*, **949**
Deceia Malloch **958**
decipiens Loew (Paralimna) *1035*
declinata Becker (Anthracophaga) 1066
decora (Loew) (Poecilographa) *930*, *931*
decora Macquart (Somula) *725*
degeerioides (Coquillett) (Admontia) *1216*, *1243*
Dejeaniopalpus Townsend 1264
deleta (Stein) (Phaonia) *1123*
deleta (Wulp) (Abapa) 1174, *1177*
Delia Robineau-Desvoidy *1103*, *1104*, *1110*, *1111*, **1112**, **1113**, **1114**
Delina Robineau-Desvoidy **1096**
Delininae 1086, 1087
delongi Johnson (Mixogaster) *730*
Delphinia Robineau-Desvoidy *800*, *803*, **805**
demandata (Fabricius) (Physiphora) *800*
demetrius D.K. McAlpine (Librella) 1072
Demoticus Macquart 1264
Dendrophaonia Malloch 1118, 1127
dentata (Coquillett) (Ceracia) 1218, *1231*
Deopalpus Townsend **1239**
depressa (Say) (Lipoptena) 1274
depressa pacifica Maa (Lipoptena) *1275*, *1278*
depressus (Shannon) (Chalcosyrphus) *725*, 734
derisa (Reinhard) (Picconia) *1216*, 1233
derivatum Walker (Chrysotoxum) *719*
Dermatobia Brauer 1150
Desmometopa Loew *903*, 904, **905**, *907*
Dettopsomyia Lamb **1012**
Deutominettia Hendel *959*, *961*, **964**
devians Hennig (Silba) 795
Dexia Meigen 1201, **1248**
Dexiinae 1193, 1196, 1200, 1201, 1221
Dexiini 1189, 1194, 1197, 1198, 1199
dexina (Townsend) (Belida) *1234*
Dexosarcophaga Townsend **1163**, *1170*
diabroticae (Shimer) (Celatoria) *1216*, *1255*
Diacrita Gerstacker **807**
Diastata Meigen *1019*, *1020*, *1021*, **1022**, 1030
Diastatidae 1009, **1019**, 1030
Dichaeta Meigen *1035*, **1039**, *1040*
Dichaetoneura Johnson 1263
Dichocera Williston 1198, *1227*, **1257**, **1261**
Diclasiopa Hendel *1032*, **1036**
Dicraeus Loew 1051, *1057*, **1060**
Dictya Meigen 928, **934**, *935*, *936*, **937**
Dictyacium Steyskal *930*, **934**
Didea Macquart **721**, *727*
Dideomima Vockeroth **723**, *727*
difficilis Gill (Heleomyza) 975
diffusa (Snow) (Gymnocarena) *818*
Dimecoenia Cresson 1029, **1044**
dimidiata (Meigen) (Rondania) *1230*, 1260
Dinera Robineau-Desvoidy *1245*, **1247**
Diocophora Borgmeier *692*, *693*, **703**, *705*, **706**
Diopsidae **785**
Diopsis 788
Diopsoidea 788
Diopsosoma Malloch 898
Diotrephes Reinhard **1206**, *1245*
Dioxyna Frey *818*, **829**
Diphuia Cresson *1034*, **1038**
Diplonevra Lioy **696**, *699*
Diplotoxa Loew *1056*, *1057*, 1064, **1065**
Discocerina Macquart 1028, 1029, *1031*, **1033**, *1037*
discolor (Cresson) (Lyciella) *959*
Discomyza Meigen 1028, **1033**
discrepans Pandellé (Phyto) *1191*
discreta (Meigen) (Pegohylemyia) 1109
disjuncta (Wiedemann) (Microphthalma) *1223*
disparifrons Borgmeier (Diocophora) *692*, *693*, *705*
dissidens group (Apallates) 1052
dissimilis (Malloch) (Neorthacheta) 1096
Distichona Wulp **1203**, *1204*
distigma Meigen (Gitona) 1012
distincta Williston (Neoascia) *727*
Ditrichophora Cresson **1038**
diversa (Coquillett) (Phasia) *1237*
diversa (Giglio-Tos) (Neorhinotora) *989*, *990*, *991*, 992
diversa (Johnson) (Platypezina) *684*
diversipennis Borgmeier (Abaristophora) *690*, *693*, 701
divisa (Meigen) (Hydrophoria) *1103*, *1104*
doclea (Walker) (Pogonortalis) 810
Dohrniphora Dahl *690*, **696**, *697*, *699*, *709*
Dolichocodia Townsend **1248**
Dolichotarsus Brooks **1233**, *1255*, **1266**
domestica Linnaeus (Musca) *1115*, *1120*, *1129*
dominicana Townsend (Ormia) *1217*, *1234*
Doros Meigen **721**
dorsalis (Coquillett) (Graphogaster) *1238*
dorsalis (Coquillett) (Myiopharus) *1237*
dorsalis (Loew) (Cerodontha) *873*
dorsalis Hendel (Dacus) 821, *822*
dorsalis Loew (Schoenomyza) *1119*
dorsata (Zetterstedt) (Pherbellia) *933*
Dorylomorpha Aczél 745, *747*, **748**
doryphorae (Riley) (Myiopharus) *1216*
Doryphorophaga 1225
Drepanoglossa Townsend **1264**
Drino Robineau-Desvoidy *1208*, **1215**, 1218, *1240*
Dromogaster Vockeroth **1096**
Drosophila Fallén *1011*, 1012, *1013*, *1014*, *1015*, **1016**, **1017**
Drosophilidae 895, 953, 1009, **1011**, 1020, 1023, 1030, 1072
Drosophilidea 1030
Drosophiloidea 917
Drymeia Meigen 1118, **1121**, *1123*, **1127**
Dryomyza Fallén *923*, 924, *925*, **926**
Dryomyzidae 922, **923**
Dryomyzinae 924, **926**
dubia Curran (Lonchoptera) 679
Dufouria Robineau-Desvoidy *1230*, **1262**
dufourii tainani Karaman (Penicillidia) *1284*, 1285
Dufouriinae 1200
duodecimpunctata Townsend (Chrysagria) 1163, *1167*
dymka (Kessel) (Seri) 683, *684*
Dyscolomyia Reinhard 1254
Dyscrasis Aldrich 799, **807**
Dyseuaresta Hendel **828**
Earomyia Zetterstedt *792*, 795, **796**
Earomyiini **795**
eburneosignata Hennig (Richardia) *833*, 837
Eccoptomera Loew **978**
Ecitomyia Brues *707*, **710**
Ectecephala Macquart *1053*, *1056*, **1065**

Eggisops Rondani 1135, 1136
Eginiini 1116, 1117
Egle Robineau–Desvoidy *1103*, **1106**, *1110*, **1111**
ehrmanni Aldrich (Hypocera) *697*, *699*
Elachiptera Macquart **1055**, *1056*, *1059*, *1063*
Elachisoma Rondani **1000**
Eldunnia Curran 1294, 1297
electrica Hennig (Glaesolonchaea) 795, 842
electrica Hennig (Pallopterites) 842
electrica Hennig (Gephromyiella) 987
electrica Hennig (Pareuthychaeta) 1022
electrica Hennig (Procremifania) 966
electrica Hennig (Prodryomyza) 924
electrica Hennig (Protoaulacigaster) 892
electrica Hennig (Protodinia) 866
electrica Hennig (Protoscinella) 1050
Electrobata Hennig 763
Electrochyliza Hennig 782
Electroclusiodes Hennig 857
Electrophortica Hennig 1012
elegans (Reinhard) (Spathidexia) 1265
elegans (Wiedemann) (Neotanypeza) *774*
elegans Coquillett (Johnsonia) *1166*, *1167*
elegans Curran (Plunomia) *968*
elegans Stein (Chelisia) 1099, 1102, *1105*
Eleodiphaga Walton *1205*, **1213**
eleodivora (Walton) (Zaira) 1198
Elfia Robineau–Desvoidy 1220
Elgiva Meigen 928, 931, **934**, *935*, *936*, **938**
Elliponeura Loew *1057*, **1065**
elongata (Fabricius) (Baccha) *714*, *719*, 721
elongatus (Hough) (Cyanus) 1144
emarginata (Say) (Epistrophella) 721
emarginata (Say) (Epistrophe) *730*, *735*
emasculator Fitch (Cuterebra) *1147*, *1155*
Emblemasoma Aldrich **1163**, *1164*, *1166*, *1170*
Emblemasomatini **1163**
Emmesomyia Malloch **1106**
Enicita Westwood *947*, **949**
Enicomira Duda *947*, **949**
enigmatica Hennig (Meoneurites) 910
Enrogalia Reinhard *1216*, **1233**
Ensina Robineau–Desvoidy 821, **826**
Eopseudopomyza 760
Eosalpingogaster Hull **720**
Eoseristalis Kanervo **741**
Epalpus Rondani *1243*, **1244**, *1246*
Ephydra Fallén *1027*, 1028, 1029, *1037*, *1042*, **1043**, *1044*, **1044**
Ephydridae 1009, 1022, **1027**, 1080
Ephydridea 1030
Ephydrinae 1027, 1028, 1029, **1030**
Ephydrini 1028
Ephydrinidae 1030
Ephydroidea 1022
Epichlorops Becker *1053*, *1061*, **1065**
epicydes (Walker) (Phebellia) *1256*
Epidexia Townsend 1214
Epigrimyia Townsend *1229*, **1264**
Epiplatea Loew 834
Epiplateinae **834**
Epistrophe Walker 720, **721**, 722, **723**, *730*, *735*
Epistrophella Dušek & Láska **721**, **723**, *730*, *735*
Epochra Loew **826**
equestris (Fabricius) (Merodon) *728*, 737
equina Fallén (Copromyza) *996*, *998*
Eremoctenia 1283
Eremomyia Stein **1109**, **1113**
Eremomyioides Malloch 1099
Eremomyioides Malloch **1102**
Eribella Mesnil *1216*, **1228**
Eribolus Becker *1059*, **1064**
Eriothrix Meigen *1230*, *1256*, **1262**
Eriozona **723**, *727*
Eristalinae 716, 717, **718**
Eristalini 716, 717
Eristalinus Rondani 718, *730*, *733*, **741**
Eristalis Latreille *728*, *733*, *740*, **741**
Ernestia 1261
Ernestia Robineau–Desvoidy 1261
Ernestiini 1261
Ernoneura Becker 1086, **1087**, *1091*
erosa Loew (Epiplatea) 834
erratica (Walker) (Callicera) *719*
erraticus (Linnaeus) (Eriozona) 723, *727*
erro Aldrich (Emblemasoma) *1164*, *1166*, *1170*
erucicola (Coquillett) (Euptilopareia) *1222*
Erucophaga Reinhard *1165*, **1178**
Ervia Robineau–Desvoidy **1262**
Erycia 1215
Eryciini 1197
Erynnia Robineau–Desvoidy *1205*, **1213**
Erynniopsis Townsend **1233**
Erythandra *1179*
Erythandra Brauer & Bergenstamm **1181**
erythrocephala (Leach) (Ornithoctona) *1275*, *1278*
erythrocera Brauer & Bergenstamm (Hesperomyia) *1240*
Estheria Robineau–Desvoidy *1219*, *1241*, **1247**, **1249**
estigmenensis (Sellers) (Hubneria) 1212
Euantha Wulp *1242*, **1249**
Euaraba Townsend *1180*, **1182**
Euaresta Loew *823*, *827*, **829**
Euarestoides Benjamin *824*, **829**
Euboettcheria Townsend **1168**
Eucalliphora Townsend **1144**
Eucampsipoda 1288
Eucelatoria Townsend **1224**, **1236**, *1238*, *1255*
eucera (Loew) (Parectecephala) *1056*
Euceromasia Townsend **1218**, *1232*
Euchaetogyne Townsend **1247**
Euclytia Townsend **1265**
Eucnephalia Townsend **1203**, *1237*
Eucoronimyia Townsend *1209*, **1218**
eucosmaphaga Arnaud (Coloradomyia) 1257
Euctenodes Waterhouse 1297
Eucyrtophloeba Townsend 1250
Eudasyphora Townsend **1121**
Eudorylas Aczél **748**
Euexorista Townsend *1204*, **1207**, *1256*
Eufrontina Brooks **1215**
Eugaurax Malloch 1051, **1052**
Euhalidaya Walton 1194, 1198, *1217*, **1225**, **1266**
Eulasiona Townsend *1209*, 1221, **1224**, **1233**
Euleia Walker **826**
Eulimosina Roháček **1003**
eulophus (Loew) (Ceratobarys) 1051, *1059*
Eumacronychia Townsend 1161, 1178, **1182**
Eumasicera Townsend **1206**, **1212**, *1232*, *1256*
Eumea Robineau–Desvoidy **1212**
Eumegaparia Townsend *1223*, *1234*, **1249**
Eumerus Meigen 718, *727*, **731**
Eumetopiella Hendel 799, *800*, 801, **806**
Eumyobia Townsend 1264
Eunemorilla Townsend *1205*, **1211**
eunota (Loew) (Melanochaeta) *1056*
Eupeodes Osten Sacken **722**, **723**, *727*, *730*, *735*
Euphasiopteryx 1264
Euphorocera Townsend 1221
Euphoroceropsis Townsend 1221
Euphyto Townsend **1181**
Euphytomima James 1161, **1181**
Eupogonomyia Malloch 1118
Euptilopareia Townsend *1222*, **1251**
Euribiinae *821*
Eurimyia Bigot *738*
Eurithia Robineau–Desvoidy 1261
Eurosta Loew *822*, **826**

Eurycephalomyia Hendel *800*, 801, *804*, **808**
Euryceromyia Townsend 1263
Eurygnathomyia Czerny 840, 842
Eurygnathomyiinae 842
eurynotus (Brues) (Aenigmatias) *697*, *705*
Euryomma Stein *1122*, **1124**
Euscopolia Townsend *1222*, **1251**
Eusenotainia Townsend **1181**
Eusiphona Coquillett 903, *906*, *907*, **908**, 1072
Eusisyropa Townsend 1206
Eustalomyia Kowarz **1106**
Eutaenionotum Oldenberg *1040*, **1041**
Euthera Loew *1230*, *1242*, **1259**
Eutheresia Townsend 1248
Euthycera Latreille 929, *930*, **934**, *935*, **938**
Euthychaeta Loew 1020, 1022, 1030
Eutreta Loew *824*, **829**
Eutrichota Kowartz 1099, *1104*, *1107*
Eutrichota Kowartz 1102, 1108
Eutrixa Coquillett *1230*, **1263**
Euxesta Loew 801, *803*, 805, **806**
evecta (Harris) (Helina) *1128*
Evidomyia Reinhard *1231*, **1263**
excavata D.K. McAlpine (Cairnsimyia) 990
exhumata Cockerell (Cordilura) 1087
exilis (Coquillett) (Epichlorops) *1053*, *1061*
exilis (Coquillett) (Eribella) *1216*
exilis (Coquillett) (Eutrixa) *1230*
exilis (Malloch) (Dorylomorpha) *747*
Exorista Meigen *1209*, **1221**, *1235*
Exoristini 1195, 1196, 1197, 1201
Exoristoides Coquillett 1220
expansa Steyskal (Dictya) *935*
extera (Cresson) (Microlytogaster) *1042*, 1043
Fabriciella 1244
fabricii Steyskal (Hoplocheiloma) 765
fallax de Meijere (Lonchoptera) 678
Fannia Robineau-Desvoidy 897, 1118, *1119*, *1122*, *1123*, **1124**, *1129*
Fanniinae 1116, 1117
farri Dodge (Sarcofahrtiopsis) *1175*
Fausta Robineau-Desvoidy 1261
femorata (Fabricius) (Ropalomera) *941*, 942
femoratus (Williston) (Brachypalpus) *725*
fenestralis (Fallén) (Aecothea) 975
fenestrata (Bigot) (Phasia) *1217*, *1252*
fenestrata (Coquillett) (Myiomyrmica) 801, *802*
fenestrata Foote (Metatephritis) 829
Ferdinandea Rondani **731**
ferrisi (Bequaert) (Neolipoptena) 1274, *1276*, *1278*, 1280
ferruginata (Stenhammar) (Coproica) *996*, *998*
ferruginea Fallén (Hammerschmidtia) 737
ferruginea Macquart (Odontomera) *835*
ferrugineus Cresson (Oidematops) *930*, 931, 937
ferrumequinum Hendel (Axiologina) 806
festivus Loew (Gaurax) *1056*, *1057*
fidelis Curran (Aecothea) 975
Fiebrigella Duda **1052**
filialis Reinhard (Cloacina) 1214
fimbriata (Waterhouse) (Myophthiria) *1275*, *1276*, 1277
finalis (Loew) (Neotephritis) *820*, *824*
flava (Linnaeus) (Chyromya) *985*, *986*
flava (Townsend) (Euclytia) 1265
flaveola (Coquillett) (Minettia) *956*, *957*
flaveola (Coquillett) (Eumegaparia) *1223*, *1234*, 1249
flaveola (Fabricius) (Dryomyza) *925*
flaveolum (Coquillett) (Astiosoma) *901*
flavescens Johnson (Sepsisoma) *835*
flaviceps (Loew) (Pseudocalliope) *955*
flavicornis Melander (Zagonia) *982*
flavida (Wiedemann) (Pachyopella) 954
flavida Coquillett (Psilopa) *1032*
flavidus Coquillett (Parepalpus) *1246*, 1247
flavifrons (Bigot) (Glyphidops) 770, *770*
flavifrons Meigen (Amauromyza) 877
flavimana Loew (Rivellia) *809*
flavipennis (Fallén) (Pycnoglossa) *1104*
flavipennis Williston (Melanophrys) *1227*
flavipes (Coquillett) (Ceranthia) *1241*
flavipes (Loew) (Xanthogramma) 721
flavipes (Meigen) (Telomerina) *1001*, *1002*
flavipes (Williston) (Zeros) *1040*
flavipes Coquillett (Prosenoides) *1232*
flavipes Linnaeus (Physocephala) *755*
flaviseta (Johnson) (Sobarocephala) *855*
flavocingulata Hendel (Cerodontha) 877
flavohalterata Malloch (Hydrophoria) *1105*
flavus Coquillett (Phasiops) 1198, *1223*, 1247
fletcheri (Aldrich) (Fletcherimyia) *1167*
fletcheri (Malloch) (Pseudocoenosia) *1119*
Fletcherimyia Townsend *1167*, **1173**
flexa (Wiedemann) (Tritoxa) 801, *802*
floralis (Fallén) (Nemorilla) 1199
floricola Borgmeier (Pericyclocera) *692*, *698*, 704
floridensis (Aldrich) (Rhytidops) *942*
floridensis (Shannon) (Monoceromyia) 729
floridensis (Townsend) (Amobia) *1179*, *1183*
floridensis Reinhard (Nicephorus) *1217*, 1248
floridensis Sabrosky (Eugaurax) 1052
floridensis Townsend (Juriniopsis) *1246*
florissantensis Cockerell (Sciomyza) 929
florum Walker (Tachina) *1193*, *1231*
foeda (Meigen) (Loewia) 1198, 1253
fontinalis (Fallén) (Leptocera) *996*, *997*, *998*
forcipata Ferris (Basilia) *1283*, 1287
Formicosepsis Meijere 760
fossulatum (Loew) (Trigonomma) *1057*, 1065
fracida Reinhard (Mactomyia) *1227*, 1260
fractiseta (Stein) (Pseudochirosia) *1103*
Francilia Shannon **1144**
frankensis Spencer (Cerodontha) 877
Frauenfeldia Egger 1189
Frendelia Collin **964**
Freraea Robineau-Desvoidy 1198, *1241*, **1254**
fricki Spencer (Liriomyza) *874*
frigida (Fabricius) (Coelopa) 920, *921*, 922
frioensis (Reinhard) (Mystacella) *1204*
frit (Linnaeus) (Oscinella) 1050, *1053*, *1056*, *1059*
frontalis (Fallén) (Trixoscelis) *982*
frontalis Curran (Eutreta) *824*
Frontiniella Townsend **1215**
fronto (Coquillett) (Myxexoristops) *1232*
fronto (Williston) (Physoconops) *752*
frontosa Say (Gonia) *1204*
Fucellia Robineau-Desvoidy **1102**
Fucelliinae 1099, **1102**
Fucomyia Haliday 922
fugax (Meigen) (Pegohylemyia) *1105*, *1110*
fulva Coquillett (Zacompsia) 806
fulviceps (Strobl) (Borboropsis) 975
fulvifrons (Macquart) (Chaetopsis) *800*, *802*
fulvifrons Say (Zodion) 751
fulvipes Cresson (Hiatus) 805
fumiferanae Tothill (Winthemia) *1237*
fumipennis (Sahlberg) (Olfersia) *1275*, *1278*
fumipennis Melander (Trixoscelis) *981*
fumosa (Egger) (Setisquamalonchaea) 796
funebris (Fabricius) (Drosophila) *1014*
fungicola group (Limosina) 1004
Fungobia Lioy 1004
furcata (Fallén) (Lonchoptera) *675*, *676*, 678, 679
furcata (Say) (Scathophaga) *1088*
furcatus Borgmeier (Bactropalpus) *709*
furcillata (Williston) (Physocephala) *752*
fuscanipennis (Macquart) (Chloroprocta) 1136, *1139*
fuscata Foote (Gonioxyna) 829
fuscipalpis (Zetterstedt) (Francilia) 1144

fuscipennis fuscipennis Loew (Sepedon) *927*, *930*
fuscipes Loew (Didea) *727*
fuscipes Zetterstedt (Cordilura) *1092*
fuscocapitata (Malloch) (Trivialia) *955*, 958
fuscus Loew (Pipunculus) *747*
futilis (Osten Sacken) (Euexorista) *1204*, 1207, *1256*
Gaediophana 1210
Gaediopsis Brauer & Bergenstamm *1204*, **1210**
galiivora Spencer (Liriomyza) 877
Ganperdea Aldrich **1108**
Gasterophilinae 1149, 1150, 1152
Gasterophilus Leach 1148, 1149, 1150, *1153*, *1154*, *1155*, **1156**, **1157**
Gastrops Williston 1028, **1030**, *1031*
Gaurax Loew *1056*, *1057*, **1058**
Gayomyia Malloch 966
gelida (Coquillett) (Chetogena) *1240*
geminata (Loew) (Jamesomyia) *823*, 828
geminatus (Say) (Toxomerus) *719*, *739*
genalis (Coquillett) (Euhalidaya) 1198, *1217*, 1225
genarum (Zetterstedt) (Acrophaga) *1137*
Genea Rondani *1231*, *1234*, **1264**
geniculata group (Leucopis) **970**
geniculata Zetterstedt (Leucopis) *969*, 970
geniseta (Malloch) (Deutominettia) *959*, *961*, 964
geometra (Robineau–Desvoidy) (Calobatina) 765, 767
Geomyza Fallén *881*, 882, *883*, *884*, **885**
Geomyzidae 1009
Gephromyiella 987
Geratomyza Spencer 872
Germaria Robineau–Desvoidy *1231*, **1266**
gibba (Loew) (Callachna) 824
Gibsonomyia Curran 1257
gigantea Cresson (Cirrula) 1028, *1037*
gigas (Sabrosky) (Neoscinella) *1054*, *1057*, *1059*
gilloglyorum Kessel (Callomyia) *687*
Gimnomera Rondani *1089*, **1093**
Ginglymia Townsend *1232*, **1239**
Gitona Meigen 1012
Gitona of American authors, not Meigen 1012, **1016**
glabra (Fallén) (Camilla) *1023*, *1024*, 1025
glabra (Meigen) (Thaumatomyia) 1050, *1053*, *1059*, *1061*
glabra Fallén (Madiza) *906*, *907*
Glaesolonchaea Hennig 795, 842
glaphyropus Loew (Athyroglossa) *1031*
glauca (Coquillett) (Oedoparena) 924
glauca (Coquillett) (Chiastocheta) *1103*
glaucellus (Stenhammar) (Hecamedoides) *1032*, 1038
Glaurocara Thomson 1198
Glenanthe Haliday *1034*, **1038**
globosa (Meigen) (Strongygaster) 1198
Glyphidops Enderlein *770*, **770**
Gnadochaeta Macquart 1198, *1226*, **1254**
Gonarcticus Becker **1095**
Gonatherus Rondani **1095**
Gonia Meigen 1199, **1203**, *1204*
Goniinae 1194, 1195, 1197, 1198, 1200, 1201
Goniini 1193, 1196, 1197, 1199, 1207
Goniocera Brauer & Bergenstammn *1226*, *1243*, **1258**
Goniochaeta Townsend *1241*, **1250**, **1254**
gonioides Coquillett (Opsidia) 1182
Goniopsita Duda 1052
Gonioxyna Hendel **829**
gonoides Townsend (Eucnephalia) 1203, *1237*
gracilipes (Loew) (Melanomyza) *955*, *960*, *962*
gracilis Fallén (Anthomyza) *887*, *888*
grahami (Aldrich) (Aldrichina) 1144
Grallipeza Rondani **765**
graminivora Sabrosky (Sacatonia) 1064
grandis Shannon (Melanodexia) *1137*, *1139*
grandis Williston (Hadromyia) *733*, 736
grandissima Sabrosky (Oscinella) 1060
Graphogaster Rondani **1221**, *1238*, *1240*
Graphogastrini 1221
Graphomya Robineau–Desvoidy *1122*, **1124**
gregaria Frick (Phytomyza) *876*
Grisdalemyia Curran 1262
grisea Coquillett (Cuterebra) 1149, *1153*
griseicollis (Becker) (Tetanocera) *930*
griseola (Fallén) (Hydrellia) 1028, *1035*, *1037*, *1042*
grisescens (Fallén) (Dinera) *1245*, 1247
griseus Brooks (Dolichotarsus) *1255*
groenlandica (Lundbeck) (Drymeia) *1123*
Grossoseta Kessel & Kirby 682, **683**, *684*, *685*
Grossovena Kessel & Maggioncalda 683, *685*, **686**
grossulariae (Meigen) (Epistrophe) *730*, *735*
Gueriniopsis Reinhard **1221**
guttatus Hardy & Wheeler (Paracacoxenus) *1013*, *1014*, 1016
guttipennis (Stenhammar) (Eutaenionotum) *1040*, 1041
guttipennis (Zetterstedt) (Anomalochaeta) *883*, 884
Gymnocarcelia Townsend **1212**
Gymnocarena Hering *818*, **826**
Gymnocheta Robineau–Desvoidy 1200, **1202**, **1260**
Gymnochiromyia Hendel *986*, **987**
Gymnoclytia Brauer & Bergenstamm *1223*, **1259**
Gymnodia Robineau–Desvoidy 1118
Gymnopalpus 1265
Gymnophora Macquart *691*, **702**, *709*
Gymnophryxe Villeneuve *1208*, **1214**
Gymnophytomyza Hendel 870
Gymnoprosopa Townsend *1180*, **1182**
Gymnopsidia Shewell *1180*, **1182**
Gymnosoma Meigen 1197, *1223*, **1259**
Gyroconops Camras **754**
Gyrostigma Brauer 1150
Hadromyia Williston 718, *733*, **736**
Haematobia Lepeletier & Serville **1118**
Haematobosca Bezzi **1118**, *1119*
haemorrhoidalis (Meigen) (Microprosopa) *1091*
haemorrhoidalis (Fallén) (Bercaea) 1162, 1169, *1171*, *1176*
haemorrhous Meigen (Paragus) 722, *735*
Haigia Steyskal **805**
Halephydra Wirth **1044**
Halidayina Duda *996*, *997*, **999**
Haloscatella Mathis *1037*, **1045**
Hammerschmidtia Schummel **737**
hannai (Cole) (Heterocheila) *925*, 926
Hapleginella Duda *1053*, *1057*, **1060**
Haplomyza Hendel 870, **878**
harringtoni (Coquillett) (Lypha) *1242*
harrisi (Reinhard) (Lypha) 1198
harrisinae (Coquillett) (Ametadoria) *1209*, 1215
harveyi (Townsend) (Bessa) 1200
hastata (Coquillett) (Eucoronimyia) *1209*, 1218
hearseiana Westwood (Sphyracephala) 788
Hebecnema Schnabl *1128*, **1130**
Hecamede Haliday 1029, *1032*, **1038**
Hecamedoides Hendel *1032*, **1038**
Hedria Steyskal 927, *930*, **934**, *936*, **938**
Helaeomyia Cresson 1029, **1036**
Helcomyza Curtis *923*, 924, *925*, **926**
Helcomyzidae 924
Helcomyzinae 924, **926**
Heleomyza Fallén *973*, 975, **979**
Heleomyzidae **973**, 982, 987, 992, 1009
Heleomyzinae 975
helicis Wirth (Platygymnopa) *1031*, 1033
Helicobia Coquillett **1169**
Helina Robineau–Desvoidy 1118, *1123*, **1126**, **1127**, *1128*, **1129**, **1130**
Heliodorus Reinhard **1214**
Heliophilus Meigen *734*, 736
Helioplagia Townsend 1220
Heloclusia Malloch 758, 760
Heloparia Enderlein 842
Helophilus Meigen *728*, **738**
Helosciomyzidae 924
helvola (Loew) (Amoebaleria) *976*, *977*

helvum (Loew) (Curtonotum) *1007*, *1008*, 1009
helymus (Walker) (Periscepsia) *1226*
hemapterus Nitzsch (Carnus) *909*, *910*
Hemeromyia Coquillett *910*, **910**
Hemiluciliini 1135
hemiptera (Curran) (Lutomyia) *976*
Hemisturmia Townsend **1206**
Hemithrixion Brauer & Bergenstamm 1266
Hemyda Robineau-Desvoidy *1217*, **1259**
hendeli Aldrich (Dyscrasis) 807
hennigi Sabrosky (Horaismoptera) 1074
hennigrata McAlpine (Leucopis) 966
Herina Robineau-Desvoidy *800*, **807**
Heringia Rondani **731**
Hershkovitzia Guimaraes & d'Andretta 1286, 1288, 1289
hesperidarum (Williston) (Spallanzania) *1208*
Hesperinus 866
Hesperomyia Brauer & Bergenstamm **1213**, *1240*
Hesperophasia 1250
Hesperophasia Townsend 1250
Hesperophasiini 1250
Hesperophasiopsis Townsend 1250
Heterocheila Rondani 924, *925*, **926**
Heteromeringia Czerny 854, *855*, **857**
Heteromyiella 975
Heteromyza Fallén 973, 975, *976*, **978**
Heteromyzidae 975
heteroneura (Haliday) (Pullimosina) 994
heteroneura (Meigen) (Taxigramma) 1182, *1183*
heteroneura group (Limosina) 1003
Hexachaeta Loew **821**
Hexamitocera Becker *1088*, **1096**
Hexomyza Enderlein **875**
hians Say (Ephydra) 1029, *1037*
Hiatomyia Shannon 718, **737**
Hiatus Cresson **805**
Hilarella *1183*
hilarella (Zetterstedt) (Actenoptera) *846*
hilarella (Zetterstedt) (Hilarella) 1182, *1183*
Hilarella Rondani 1161, 1178, **1182**
hilarella Zetterstedt (Phytoliriomyza) 877
Himeroessa Loew **810**
Hinei (Malloch) (Delia) 1114
Hineomyia Townsend **1261**
Hippelates Loew **1052**, *1061*, **1064**
Hippobosca Linnaeus **1274**, *1276*, *1279*
Hippoboscidae **1271**, 1289, 1297
Hippoboscidae auct. 1297
Hippoboscinae **1274**, 1297
hirsuta (Ferris) (Icosta) 1274
hirsuta Coquillett (Omomyia) 833, 834, *835*
hirtifrons Peterson & Robinson (Zyziphora) *692*, 703
hirtus Loew (Tetropismenus) 808
hispida (Basilia) 1288
hispida Theodor (Basilia) 1287
Homalactia Townsend 1220
Homalocephala Zetterstedt *800*, 801, **805**
Homaluroides Sabrosky **1065**
Homaroides Malloch 842
hominis Linnaeus Jr. (Dermatobia) 1150
hominivorax (Coquerel) (Cochliomyia) 1135
Homoneura Wulp 953, **954**, *957*, *960*, *961*, *963*
Homoneurinae 953
hondurana Steyskal (Epiplatea) 834
Hoplocheiloma Cresson **765**
Hoplodictya Cresson **934**, *935*, *936*, **937**
Horaismoptera Hendel 1074, 1075
horripilans (Melander) (Tethina) *1076*, *1077*
houghi Malloch (Macrophorbia) **1106**
Houghia Coquillett 1206
housei Shewell (Agria) 1181, *1183*
Hubneria Robineau-Desvoidy **1212**
Huckettia Vockeroth **1095**
huidobrensis (Blanchard) (Liriomyza) 871
humeralis (Stein) (Eutrichota) *1107*
humilis (Zetterstedt) (Brontaea) *1123*
hunteri (Hough) (Protodexia) *1167*, *1172*, 1173, *1176*
hurdi Sabrosky (Phyllomyza) 904
Hyadina Haliday 1028, *1035*, **1043**
Hyalomya Robineau-Desvoidy 1258
Hyalomyodes Townsend 1260
Hyalurgus Brauer & Bergenstamm **1261**
Hybomitra 1198
hybreas (Walker) (Ceromasia) *1217*
Hydrellia Robineau-Desvoidy 1028, 1029, *1035*, *1037*, **1039**, *1042*, *1044*
Hydrelliinae 1027, 1028, 1029, **1039**
Hydrina Robineau-Desvoidy 1041
Hydrochasma Hendel *1031*, **1033**
Hydromyza Fallén 1085, 1086, *1089*, **1093**
Hydrophoria Robineau-Desvoidy *1103*, *1104*, *1105*, **1106**, **1109**, **1113**
Hydropyrus Cresson *1037*, **1043**
Hydrotaea Robineau-Desvoidy 1118, *1120*, *1123*, **1126**, **1127**, **1128**
Hylemya Robineau-Desvoidy *1101*, **1108**
Hylemyza Schnabl & Dziedzicki **1108**
hylotomae (Coquillett) (Vibrissina) *1209*
Hypenomyia 1249
hyperboreus (Greene) (Amphipogon) *846*, *848*, 852
Hypertrophocera Townsend *1223*, **1253**
Hypertrophomma Townsend **1212**, *1232*
hyphantriae (Tothill) (Blondelia) *1245*
Hyphantrophaga Townsend **1206**, **1207**, *1252*
Hypocera Lioy *697*, *699*, **701**
Hypocerides Schmitz *690*, *697*, **701**
Hypocerina Malloch *697*, **701**, *709*
Hypoderma Latreille 1148, 1149, 1150, 1152, *1153*, *1154*, *1155*, **1156**, **1157**
Hypodermatinae 1149, 1150, 1152, 1156
hypopygialis (Townsend) (Microcerella) *1167*, *1172*
Hypovoria Villeneuve *1219*, **1250**
hyrtlii (Kolenati) (Eucampsipoda) 1288
Hystricia Macquart 1195, 1201, **1202**, **1220**, *1243*
Icaridion Lamb 922
Icerya 1072
iceryae (Williston) (Cryptochetum) *1069*, *1070*, 1072
Icosta Speiser 1274, *1275*, *1276*, **1277**, *1278*
Icterica Loew *823*, **826**
Ictericophyto Townsend 1258
Idana Loew 806, 807, **808**
idessa (Walker) (Graphomya) *1122*
Idoneamima Dodge 1168
ignava (Harris) (Hydrotaea) *1120*
illustris (Meigen) (Lucilia) *1138*, 1140
Ilythea Haliday *1034*, **1039**, *1040*
Imaguncula Reinhard 1203
Imitomyia Townsend 1196, *1229*, **1260**
immaculata (Macquart) (Gymnoclytia) *1223*
Impariini 1162, **1173**
Impeccantia Reinhard *1231*, **1266**
importuna (Walker) (Metoposarcophaga) *1175*
impressa (Bigot) (Stilbometopa) *1276*, *1278*
inaequata Namba (Rivellia) *811*
inaequipes Bigot (Cholomyia) 1265
incanus Reinhard (Isidotus) 1263
incerta (Becker) (Incertella) *1053*
Incertella Sabrosky *1053*, **1064**
incompta Vockeroth (Dromogaster) 1096
incongruus Aldrich (Dicraeus) *1057*
indecora (Loew) (Pholeomyia) *907*
iners (Meigen) (Schroederella) 975
infida Reinhard (Evidomyia) *1231*, 1263
inflata (Macquart) (Palumbia) 741
inflaticornis (Allen) (Gymnopsidia) *1180*, 1182
ingratus (Loew) (Dicraeus) 1051
innocuus (Zetterstedt) (Thricops) *1123*
innota (Walker) (Sarcodexia) *1171*
inquilinus (Coquillett) (Chaetochlorops) 1052, *1061*

insignis Aldrich (Calotarsa) *684*, *685*, *687*
integre Williston (Chrysotoxum) *735*
interior Chillcott (Glenanthe) *1034*
intermedia Walker (Scathophaga) *1091*
intermedium Banks (Zodion) *752*
interrupta Curran (Actia) *1238*, *1241*
intersecta (Meigen) (Pseudonupedia) *1105*, 1109
intestinalis (De Geer) (Gasterophilus) *1153*, *1154*, *1155*
intrudens (Curran) (Siphona) *1232*
io (Aldrich) (Goniocera) *1226*, *1243*, 1258
iroquoiana (Malloch) (Megaselia) *705*
irritans (Linnaeus) (Haematobia) 1118
irrorata Coquillett (Traginops) 864, *865*
Ischiodon Sack 715
Ischiolepta Lioy *998*, **1004**
Ischnomyia Loew **890**
Ischyrosyrphus Bigot **722**
Isidotus Reinhard **1263**
Istocheta Rondani *1209*, **1224**
jaceana (Hering) (Urophora) *822*
jaegeri Hennig (Phyllomyza) 904
jamaicensis Dodge (Sarcofahrtiopsis) *1176*
Jamesomyia Quisenberry *823*, **828**
Jantia Rohdendorf 1169
Japanagromyza Sasakawa 869, 870, **872**
Jassidophaga Aczél **748**
javana Brauer & Bergenstamm (Chaetexorista) 1221
Jaynsleskia Townsend 1264
johnsoni (Aldrich) (Wohlfahrtiopsis) *1171*
johnsoni (Spuler) (Thoracochaeta) 994
johnsoni (Stein) (Leucophora) *1107*
johnsoni Darlington (Porsenus) 977
Johnsonia Coquillett *1166*, *1167*, *1175*, **1178**
Johnsoniini 1161, **1178**
Jurinella Brauer & Bergenstamm **1244**
Jurinia Robineau–Desvoidy **1244**
Juriniopsis Townsend **1244**, *1246*
kahli Kessel (Melanderomyia) 683, *687*
kallima group (Phytobia) 877
karli Hendel (Amauromyza) *874*
Katacamilla Papp 1025
katmaiensis (Malloch) (Nanna) *1092*
keeniana Williston (Sphegina) *725*, *728*
kellyi (Aldrich) (Kellymyia) *1176*
Kellymyia Townsend *1166*, **1174**, *1176*
Kimosina Roháček **999**, *1001*
kincaidii (Coquillett) (Pyritis) *726*
Kirbya Robineau–Desvoidy *1219*, *1238*, **1250**
knabi Shannon (Syrphus) *740*
kuehnei Hennig (Eopseudopomyza) 760
l'hoesti Meunier (Palaeotimia) 924
labiatarum Hering (Ophiomyia) *874*
labis (Coquillett) (Xanthophyto) *1235*
lacteipennis (Loew) (Diclasiopa) *1032*, 1036
lacteipennis (Loew) (Milichiella) *906*, *907*
lacteipennis (Malloch) (Pseudonapomyza) *873*
laetifica Spencer (Melanagromyza) *873*
laetus (Loew) (Parhelophilus) *728*, *735*
laevigata (Meigen) (Leiomyza) *901*
laevis Loew (Allophyla) 975
lampra Steyskal (Cinderella) 978
Lamprolonchaea Bezzi *792*, 795, **796**
Lamproscatella Hendel *1037*, **1045**, **1046**
lapponicus (Zetterstedt) (Eupeodes) *727*
Lapposyrphus Dušek & Láska **722**, *727*
laricis Momoi (Cephaloglypta) 1199
larssoni Hennig (Xenanthomyza) 892
larvarum (Linnaeus) (Exorista) *1209*
lasciva (Fabricius) (Taeniaptera) *766*, 767
Lasiomma Stein *1103*, *1104*, **1111**, **1112**, **1114**
Lasionalia Curran 1224
Lasioneura Coquillett 1239
lasiophthalma (Zetterstedt) (Melangyna) *735*
Lasiopiophila Duda 845, *848*, *851*, **851**
Lasiopleura Becker 1051
Lasioscelus Becker **1094**
Lasiosina Becker **1066**
lateralis (Fallén) (Napomyza) *873*
lateralis (Walker) (Clusia) *853*, *856*
lathami (Curran) (Calolydella) 1197
Latheticomyia Wheeler *757*, 758, *759*, 760
laticauda Loew (Steneretma) 801, *802*
latifrons (Hough) (Eucalliphora) 1144
latifrons (Loew) (Dasyopa) *1054*
latifrons Loew (Helophilus) *728*
latigena Wood (Ligeria) 1228
latipennis (Coquillett) (Steganolauxania) *957*, *960*
latipennis (Zetterstedt) (Acrostilpna) 1112
latipennis Aldrich (Meledonus) *1226*
latipes (Meigen) (Leptometopa) *906*, *907*
latipes (Meigen) (Protopiophila) *848*, 852
latisterna Parker (Boettcheria) *1166*, *1167*, *1175*
latiusculus (Loew) (Ceroxys) *799*, *802*, 808
Lauxania Latreille 953, *956*, **958**
Lauxaniella Malloch *956*, **958**
Lauxaniidae **951**
Lauxanioidea 917
Lecanocerus Borgmeier *691*, *697*, 702, **703**, **704**
Leiomyza Macquart 899, *901*, **900**
Lejops Rondani *726*, *733*, *735*, **738**, **741**
Lejota Rondani **732**, **736**
Lemnaphila Cresson 1029, *1035*, **1041**
Lemurimyza Spencer *872*
Lenkokroeberia Prado 941
lepida (Meigen) (Rhinophora) 1189
Lepidomyia Loew 715, *724*, **729**
Leptocera Olivier **995**, *996*, *997*, **997**, *998*, *1002*
Leptometopa Becker 904, **905**, *906*, *907*
Leptopsilopa Cresson *1032*, **1036**
Leriola Gorodkov 975
Leschenaultia Robineau–Desvoidy **1213**, *1243*
Leskia Robineau–Desvoidy *1230*, **1264**
Leskiella James 1264
Leskiini 1194
Leskiomima Brauer & Bergenstamm 1264
Leskiopsis Townsend *1235*, **1264**
Lespesia Robineau–Desvoidy **1211**, **1213**, **1215**, *1237*
leucaniae (Coquillett) (Patelloa) *1234*
leucopeza (Meigen) (Aulacigaster) *891*, 892, *893*
leucophaeata (Reinhard) (Eucelatoria) *1238*
Leucophenga Mik 1012, **1016**
Leucophora Robineau–Desvoidy *1103*, *1107*, **1112**, **1113**
leucophrys (Wiedemann) (Leschenaultia) *1243*
Leucopini **967**
Leucopis Meigen 965, 966, **967**, *968*, *969*, *970*, **970**
Leucopodella Hull **721**
Leucopomyia Malloch *969*, **970**
leucoprocta (Wiedemann) (Bithoracochaeta) 1125
leucoproctum (Loew) (Hydrochasma) *1031*
leucoptera (Johnson) (Neaera) *1235*
Leucostoma Meigen 1195, 1196, *1243*, **1251**, *1252*, **1259**, 1263
Leucozona Schiner **722**
levida (Harris) (Muscina) *1122*
Librella D.K. McAlpine 1072
Ligeria Robineau–Desvoidy **1228**
limata (Coquillett) (Zizyphomyia) 1218
limenitis Steyskal (Pherbecta) 934, 937
Limnellia Malloch **1045**
Limnia Robineau–Desvoidy **934**, **938**
Limnophora Robineau–Desvoidy 1118, **1124**
Limnospila Schnabl *1119*, **1126**
limosa (Fallén) (Leptocera) *997*, *998*
Limosia Robineau–Desvoidy *1123*, **1126**
Limosina complex 995
Limosina Macquart 999, 1000, 1003, 1004
Limosininae 994, **995**

Lindneromyia Kessel 683
lindsleyi Sturtevant & Wheeler (Asmeringa) 1038
linearis (Townsend) (Sphaerina) 1225
lineata Van Duzee (Micropeza) *761*, *764*
lineata Wheeler (Latheticomyia) 758
lineatum (Villers) (Hypoderma) 1150, *1155*
lineolatus (Wiedemann) (Telostylinus) 770
Linnaemya Robineau–Desvoidy *1227*, **1257**, **1260**
Liohippelates Duda **1051**, *1061*
Liopiophila Duda *848*, **852**
Liopygia Enderlein **1169**, *1176*
Liosarcophaga Enderlein **1168**
Lioscinella Duda **1060**
Lipara Meigen 900, 1049, 1050, **1052**
Lipochaeta Coquillett 1027, *1034*, **1039**
Lipoleucopis Meijere 966, **967**, *968*
Lipoptena Nitzsch 1272, 1273, 1274, *1275*, *1278*, **1280**
Lipopteninae **1274**
Liriomyza Mik 870, 871, 872, *873*, *874*, *876*, **877**, **878**
Lispe Latreille 1116, **1118**, *1119*
Lispideosoma Townsend 1220
Lispocephala Pokorny 1118, 1125
Lispoides Malloch *1123*,**1126**
Listriomastax Enderlein 1075
Litophasia Girschner 1200
litoreus (Enderlein) (Apetaenus) 1075
littoralis (Malloch) (Tetramerinx) *1120*
littorea (Hutton) (Macrocanace) 1074
litturata (Olivier) (Euantha) *1242*, 1249
lituratus (Loew) (Teuchocnemis) *728*, *735*
livida Hall (Calliphora) *1142*
Lixophaga Townsend 1197, 1198, **1233**, *1235*, **1236**, *1256*
Lochmostyliinae 814
loewi Meunier (Palaeosicus) 751
Loewia Egger 1198, **1253**
Loewimyia Sabrosky 899, *901*, **902**
Lonchaea Fallén *791*, *793*, *794*, 795, **796**, 954
Lonchaeidae **791**, 801, 840, 842
Lonchaeinae **795**
Lonchaeini **795**
Lonchaeoidea 917
Lonchoptera Meigen *675*, *676*, 678, 679
Lonchopteridae **675**
lonchopteroides Walker (Cadrema) 679
longiceps Sabrosky (Bahamia) 900
longicornis (Coquillett) (Odontoloxozus) *769*, *770*
longicornis (Coquillett) (Pseudocalliope) *955*
longicornis (Reinhard) (Eunemorilla) *1205*
longicornis (Sturtevant & Wheeler) (Pseudohyadina) 1043
longicornis Bigot (Stictomyia) *802*
longifrons (Brues) (Phalacrotophora) *692*, *700*, 706
longimana Fallén (Tanypeza) *773*, *774*
longinasus Shannon (Cynorhinella) *727*, *733*
longipennis (Loew) (Suillia) *976*
longipennis (Wiedemann) (Strauzia) *818*, *820*, 826
longipennis Fabricius (Hippobosca) 1274, *1276*, *1279*
longipennis Loew (Mycetaulus) *846*, *848*, *850*
longipes (Loew) (Stenoscinis) *1054*, *1056*
longirostris Johnson (Rhynencina) 821
longiterebra Hennig (Latheticomyia) *759*
longus (Walker) (Cosmetopus) *1091*, 1094
Lopesiodinia Prado 866
Lophosceles Ringdahl *1120*, **1129**
loriola (Reinhard) (Trochiloleskia) 1264
Lotophila Lioy **1004**
Loxocera Meigen **782**, *783*, **784**
loxocerata (Fallén) (Hexamitocera) *1088*, 1096
loxodontis Rodhain (Ruttenia) 1150
lucens Meigen (Lipara) 1050, 1052
Lucilia Robineau–Desvoidy 1135, *1138*, **1140**
Luciliini 1135, **1140**
lucorum (Linnaeus) (Leucozona) 722
luctuosa (Meigen) (Cerodontha) *873*
luctuosum Meigen (Orygma) 946, *947*
ludens (Loew) (Anastrepha) *820*, *822*
lunata (Fabricius) (Stomorhina) *1139*, 1140
Lunomyia Curran & Fluke *726*, **741**
lupulina (Fabricius) (Minettia) *951*, *962*
lurida (Loew) (Geomyza) *881*, *883*, *884*
lurida (Meigen) (Suillia) 975
lustrans (Reinhard) (Catharosia) *1242*
lutea Panzer (Lonchoptera) 678, 679
luteata (Haliday) (Allopiophila) *846*, *848*, 852
luteisquama (Zetterstedt) (Helina) 1129
luteiventris Schmitz (Gymnophora) *691*, *709*
luteoala (Garrett) (Schroederella) 975
Lutomyia Aldrich 973, 975, *976*, **978**
lutosa group 997
lutzi Curran (Jurinella) 1244
Lyciella Collin **954**, *959*
Lydella Robineau–Desvoidy 1197, *1208*, **1215**
Lydina Robineau–Desvoidy 1195, **1220**
Lynchia Weyenbergh 1274
Lypha Robineau–Desvoidy 1195, 1198, 1201, **1220**, *1242*, *1243*, **1257**
Lyphini 1188
Lyphini 1188, 1220
Lytogaster Becker 1029, **1043**
m–nigrum (Zetterstedt) (Desmometopa) *903*, *907*
mabelae (Cresson) (Ptilomyia) *1034*
macateei (Malloch) (Canacea) *1079*, 1080, *1081*, *1082*
Macateeia Malloch **1112**
macellaria (Fabricius) (Cochliomyia) 1136, *1137*, *1139*
Macquartia Robineau–Desvoidy 1195, 1196, 1201, *1226*, **1258**, **1262**
Macrocanace Tonnoir & Malloch 1074, 1075, 1080
Macromya Robineau–Desvoidy 1201, **1202**, *1234*
Macronychia Rondani 1160, 1161, *1179*, **1181**
Macrophorbia Malloch **1106**
macrophylli Wenzel (Trichobius) 1297
macropi Froggatt (Tracheomyia) 1152
macropogon (Bigot) (Menetus) *1222*, 1251
macropus Walker (Sepedomerus) 934
Macrorchis Rondani **1126**
Mactomyia Reinhard *1227*, **1260**
macula (Loew) (Poecilominettia) *956*
maculata (Cresson) (Pherbellia) *930*
maculata (Stein) (Leucophora) *1103*
maculata Meigen (Odinia) 864
maculipennis (Becker) (Heleomyza) 975, 979
maculipennis (Spuler) (Spelobia) 1000
Madiza 1058
Madiza Fallén **905**, *906*, *907*
madizans (Fallén) (Trimerina) 1029, 1036, *1042*
Madizinae 903, 904, **905**
Madremyia Townsend **1211**
magna Brooks (Onychogonia) *1208*
magnipalpis (Aldrich) (Woodiphora) *691*, 702
major (Coquillett) (Trichobius) 1296, 1297, *1299*
Malacomyia Haliday 922
mallochi (Sabrosky) (Speccafrons) *1053*, 1058
mallochi (Sturtevant) (Pelomyiella) *1076*, *1077*
Mallochomyza Hendel *959*, *961*, **963**
Malloewia Sabrosky *1054*, **1058**
Mallota Meigen *714*, **738**
manca (Greene) (Chaetostigmoptera) 1233
manitobensis Curran (Microdon) *739*
Mantidophaga Townsend **1173**
mantis (De Geer) (Ochthera) *1042*
manuleata (Loew) (Melanomyza) *956*
Maorimyia Tonnoir & Malloch 924
Marbenia Malloch 898
marginalis Curran (Arctophyto) *1223*
marginata (Say) (Physocephala) 751
marginata (Say) (Idana) 808
marmorata (Bigot) (Leucopodella) 721

martini Spencer (Melanagromyza) *874*
Masiphya Brauer & Bergenstamm 1198, **1215**, *1232*
Masiphyini 1215
Masiphyomyia 1211
Masiphyomyia Reinhard 1211
Masistylum *1240*
Masistylum Brauer & Bergenstamm **1215**
Masoniella Vockeroth **1075**, *1076*, *1077*
matthewsi Steyskal (Dictya) *936*
maura (Meigen) (Ophiomyia) *873*
Mauromyia Coquillett *1222*, **1253**
mcalpinei Hennig (Morgea) 795, 842
Mecynocorpus Roback **1168**, *1170*
Medina Robineau–Desvoidy 1197, 1201, *1217*, **1225**, *1252*
meditabunda (Fabricius) (Myospila) 1124
Megachetum Rondani **782**
Megamerinidae 788
Megaparia Wulp **1248**
Megapariopsis Townsend *1234*, *1241*, **1249**
Megaphthalma Becker **1093**
Megaphthalmoides Ringdahl **1095**
Megaprosopus Robineau–Desvoidy **1254**
Megaselia Rondani 695, *705*, **706**, **708**, *709*
Megasyrphus Dušek & Láska **723**
Megistopoda Kolenati 1296, 1297
Meigenia Robineau–Desvoidy 1197, 1201, **1224**, *1235*
Meigenielloides Townsend 1198, **1233**
Melaleucopis Sabrosky 966
Melanagromyza Hendel 869, 870, 871, 872, *873*, *874*, **875**, *876*
Melananthomyza Malloch 890
melancholica Becker (Oscinella) 1060
melanderi Brues (Acontistoptera) *693*, *698*, *700*, 710
melanderi Cockerell (Nomia) 1161
Melanderomyia Kessel **683**, *684*, **686**, *687*
Melangyna Verrall **722**, **723**, *735*
Melanochaeta Bezzi **1055**, *1056*
Melanodexia Williston *1137*, *1139*, **1140**
melanogaster Meigen (Drosophila) *1011*, *1015*
Melanoloma Loew 833, 834
Melanomya Rondani 1136, 1188
Melanomyza Malloch *955*, *956*, **958**, *960*, *962*
Melanophora Meigen *1187*, 1188, 1189, *1191*, **1191**, **1251**
Melanophrys Williston *1227*, **1261**
Melanophytobia Hering 872
melanoptera (Fallén) (Morinia) 1188
melanoptera (Meigen) (Anthracomyia) 1188
Melanostoma Schiner 718, *719*, **721**, *730*
melanura (Loew) (Acidogona) 826
melanura (Meigen) (Bellieria) *1164*, 1169, *1171*
Meledonus *1226*
Meledonus Aldrich **1254**
Melieria Robineau–Desvoidy 799, **807**
Meligramma Frey **722**, **723**
Melinda Robineau–Desvoidy 1136
Melinocera Townsend 1261
Meliscaeva Frey 718, **720**, *730*
mella (Walker) (Exorista) *1235*
mellifera Linnaeus (Apis) 751
mellinum (Linnaeus) (Melanostoma) *719*, 721, *730*
Melophaginae Bezzi 1274
Melophagus Latreille 1272, 1273, 1274, *1279*, **1280**
Menetus *1222*
Menetus Aldrich **1251**
menthae Spencer (Calycomyza) *874*
Meoneura Rondani 909, *910*, **910**
Meoneurites 910
meralis Reinhard (Clastoneuriopsis) 1221, *1230*
Merapioidus Bigot *725*, **736**
Mericia Robineau–Desvoidy 1261
meridiana Hendel (Calycomyza) 877
Merodon Meigen 718, *728*, **737**
Merodontini 715, 716, 717
Meromacrus Rondani **741**
Meromyza Meigen 1050, *1061*, **1064**
Meropliosepsis Duda 946, **949**
Meroplius Rondani *947*, **949**
Mesembrina Meigen **1121**
Mesembrinella Giglio–Tos 1135
Mesembrinellinae 1136
Mesophora Borgmeier **703**
Mesosphaerocera Kim *997*, **1004**
Metaclythia Kessel **683**, *684*
Metadexia Coquillett 1249
metallica (Cole) (Rhinonapaea) 1041
metallica (Williston) (Neoascia) *724*
Metamyia Arnaud 1257
Metaphyto Coquillett 1261
Metaplagia Coquillett **1250**
Metasyrphus 723
Metatephritis Foote **829**
Metavoria Townsend 1250
Metopia *1180*
Metopia Meigen **1185**
Metopina Macquart *693*, *698*, **708**
Metopininae 695, **696**, **702**
Metopinini 695, **702**
Metopiops Townsend 1210
Metopomuscopteryx Townsend *1226*, **1258**
Metopomyza Hendel **877**
Metoposarcophaga Townsend **1174**, *1175*
Metopotachina Townsend 1244
meunieri (Hendel) (Electroclusiodes) 857
mexicana (Wiedemann) (Dyseuaresta) 828
mexicana Malloch (Stenopyrgota) 814
mexicana Steyskal (Mexicoa) *942*
mexicanum Borgmeier (Xanionotum) *700*
mexicanus Curran (Xanthandrus) 721, *730*
Mexicoa Steyskal 941, *942*, **942**
Miamimyia Townsend **1239**
micheneri (Fluke) (Lepidomyia) *724*, 729
micidus Reinhard (Opsidiotrophus) 1182
Microcerella Macquart *1167*, *1172*, **1174**
Microcerellini 1161, **1174**
Microchaetina Wulp **1220**, *1234*, *1241*, **1249**
Microdon Meigen 717, 718, *727*, **729**, *730*, *733*, *739*, *740*
Microdontinae 713, 715, 716, 717, **718**
Microdontini 717
Microdrosophila Malloch *1013*, **1017**
Microlynchia Lutz, Neiva, & Lima *1275*, **1277**, *1278*
Microlytogaster Clausen 1028, 1030, *1042*, **1043**
Micromintho Townsend 1218
Micropeza Meigen *761*, 763, *764*, **765**
Micropezidae **761**
Micropezinae 761, **765**
Microphthalma Macquart *1223*, **1254**
Microprosopa Becker *1091*, **1095**
micropyga Duda (Ischiolepta) *998*
Microsania Zetterstedt 682, **683**, *684*
Microselia Schmitz 696
Microtarsina Schiner 1188
Milesia Latreille 718, *728*, **732**
Milesiinae 717
Milesiini 716
Milichia Meigen 903, **908**
Milichiella Giglio–Tos *906*, *907*, **908**
Milichiidae **903**, 910, 1072, 1075, 1080
Milichiinae 903, 904, **905**
Milichioidea 917
Miltogramminae 1160, 1161, 1162, **1163**, *1179*, *1180*, *1183*, 1200
Miltogrammini 1160, 1161, 1162, **1178**
mima (Hennig) (Compsobata) *764*
mimetica (Malloch) (Craspedochoeta) 1109, 1112
Mimologus Reinhard 1211
mimoni Theodor & Peterson (Basilia) 1288
Minettia Robineau–Desvoidy *951*, 953, *956*, *957*, *962*, **964**
Minilimosina Roháček **1000**, *1001*, 1002, **1004**

minima (Strobl) (Calamoncosis) *1053*
minor (Haliday) (Enicomira) *947*, 949
Minthodexiopsis Townsend 1265
Minthozelia Townsend 1249
minuta (Meunier) (Pareuthychaeta) 1022
minutissima group (Limosina) 1003
miocenica (Cockerell) (Thelida) 975
miocenica (Heteromyiella) 975
mira Coquillett (Eusiphona) *906*, *907*
mirabilis (Collin) (Opalimosina) 1003
mirabilis Melander (Helcomyza) *923*, *925*, 926
mitis (Curran) (Cyzenis) *1238*
mitis (Reinhard) (Cinochira) 1263
Mixogaster Macquart **729**, *730*
mixta Steyskal (Hedria) *930*, 934, *936*, 938
Mochlosoma Brauer & Bergenstamm **1248**
modesta (Wiedemann) (Argoravinia) 1163
modesta (Zetterstedt) (Protoclythia) *684*
mogollonensis Kessel & Kessel (Symmetricella) *685*, 686
mollis Becker (Scathophaga) 1086
Monoceromyia Shannon **729**
Monochaetoscinella Duda *1054*, **1055**
montana (Coquillett) (Freraea) *1241*, 1254
montana (Shannon) (Acronesia) *1139*
montana Day (Tetanocera) *936*
montanensis (Parker) (Toxonagria) *1179*, 1181, *1183*
Morellia Robineau–Desvoidy **1121**, *1122*
Morgea Hennig 795, 840, 842
morigera Reinhard (Enrogalia) *1216*, 1233
Morinia Robineau–Desvoidy 1188
Mormotomyiidae 917
Morpholeria Garrett 975, **979**
Mosillus Latreille *1034*, **1039**
Mumetopia Melander *888*, *889*, **890**
muria Mathis (Lamproscatella) *1037*
Musca Linnaeus *1115*, 1117, *1120*, **1121**, *1129*, 1136
muscaria (Fabricius) (Egle) *1103*, *1110*
muscaria (Loew) (Xenochaetina) *955*, *957*, 958, *960*
Muscidae 1100, **1115**, 1136, 1149, 1087, 1189
Muscina Robineau–Desvoidy *1122*, **1128**
Muscinae 1117, 1195
Muscini 1117
Muscomorpha 864, 910, 1150
Muscopteryx Townsend **1253**, **1258**
Musidora Meigen 679
Musidoridae 679
Myatelemus Reinhard *1208*, **1214**
Mycetaulini 847
Mycetaulus Loew 845, *846*, 847, *848*, *850*, **852**
Mycodrosophila Oldenberg **1012**, *1013*
Mydaea Robineau–Desvoidy **1124**
Mydaeina Malloch 1118
Myioclonia Reinhard 1258
Myiomyrmica Steyskal **801**, *802*
Myiopharus Brauer & Bergenstamm *1216*, **1225**, **1228**, **1233**, *1237*
Myiophasia 1254
Myiophthiria 1274
Mylogymnocarena Foote **826**
Myobiopsis Townsend 1264
Myoleja Rondani 821, **826**
Myolepta Newman *724*, **729**, *733*
Myopa Fabricius 750, *752*, **754**, *755*, **756**
myopaeformis (Roder) (Tetanops) *800*, 801, *804*, 808
Myophthiria Rondani 1272, 1274, *1275*, *1276*, **1277**
Myopina Robineau–Desvoidy **1102**
Myopinae 749, 750, 751, **754**, **756**
Myopinini **1102**
Myopitinae **821**
Myospila Rondani **1124**
Myothyriopsis Townsend **1218**, *1242*, *1243*
myotis Curran (Basilia) 1287
myrmecoides (Loew) (Myrmecothea) 801, *802*
Myrmecothea Hendel 799, **801**, *802*
Myrmosicarius Borgmeier *692*, *697*, *700*, **703**, *705*
Mystacella Wulp *1204*, **1210**
Mystacomyia Giglio–Tos **1211**, *1234*
Myxexoristops Townsend **1207**, *1232*
nana (Zetterstedt) (Eribolus) *1059*
Nanna Becker 1087, *1092*, **1096**
Napomyza Westwood 870, *873*, **878**
nasica Say (Rhingia) *724*, 731
nasoni (Cresson) (Cnodacophora) *762*, *764*
nasoni Coquillett (Admontia) 1228
Nausigaster Williston 715, **731**, *733*
Neaera Robineau–Desvoidy *1235*, **1263**
nearctica (Parker) (Robineauella) *1165*, *1171*, *1177*
nearctica Vockeroth (Huckettia) 1095
Nearcticorpus Roháček & Marshall 995, **999**, 1003
nearcticus Borgmeier (Hypocerides) *690*, *697*, 701
Neaspilota Osten Sacken **825**
nebularum Aldrich (Coelopa) *921*
nebulosa (Coquillett) (Sphenometopa) *1180*
nebulosa (Loew) (Grallipeza) 765
nebulosa Melander (Cyamops) *893*
nebulosus Coquillett (Gastrops) *1031*
necrophila Albuquerque (Bocainamyia) *846*
neglecta Williston (Stylogaster) *752*, *753*
Nemopoda Robineau–Desvoidy *947*, **949**
Nemorilla Rondani 1199, 1200, **1206**
Nemorimyza Frey 870, **877**
Neoalticomerus Hendel 863, 864, **866**, *867*
Neoascia Williston 717, *724*, *727*, **732**
Neobellieria Blanchard 1161, *1176*, **1169**
Neochirosia Malloch 1086, *1089*, *1092*, **1096**
Neocuterebra 1150
neocynipsea Melander & Spuler (Sepsis) *949*
Neodeceia Malloch *955*, **958**
Neodexiopsis Malloch *1123*, **1126**
Neodichocera Walton 1257
Neodiplotoxa Malloch **1064**
Neodohrniphora Malloch *691*, *697*, **702**
Neoecothea Peterson & Gill 975
Neofischeria Townsend 1264
Neogimnomera Malloch **1093**
Neogriphoneura Malloch **954**, *956*, *960*, *961*
Neohydrotaea Malloch 1118
Neohylemyia Malloch **1108**
Neoleria Malloch **979**
Neoleucopis Malloch 965, 966, **967**, *968*
Neolipoptena Bequaert 1272, 1273, 1274, *1276*, *1278*, **1280**
Neomaorina Miller 842
Neomintho Brauer & Bergenstamm **1218**, *1238*
Neominthoini 1218
Neomuscina Townsend *1120*, **1121**, *1122*
Neomyia Walker 1118, **1121**, *1122*
Neopelomyia Hendel 1074, **1075**, *1076*
Neophyllomyza Melander **905**, *907*
Neophyto Townsend *1165*, *1175*, **1178**
Neophytoini **1178**
Neopiophila McAlpine 845, *846*, 847, *848*, *849*, 851, **852**
Neorhinotora Lopes *989*, *990*, *991*, 992
Neorthacheta Vockeroth **1096**
Neosarcophaga Shewell **1168**
Neoscatella Malloch **1045**
Neoscinella Sabrosky *1054*, *1057*, *1059*, **1060**
Neoscutops Malloch 897, 898
Neosilba McAlpine *792*, *793*, **796**
Neosolieria Townsend **1261**
Neossos Malloch 975, 978, **979**, 982
Neotanygastrella Duda 1012
Neotanypeza Hendel *774*, **776**
Neotephritis Hendel *820*, *824*, **829**
Neotraginops Prado 864, 866
Neottiophilinae 847, **851**
Neottiophilum Frauenfeld *846*, 847, *848*
nepenthe (Hull) (Eosalpingogaster) 720

Nephrocerini 745, **748**
Nephrocerus Zetterstedt 745, 746, *747*, **748**
Neplas Porter 718, *725*, *733*, **734**
Neriidae **769**
Neriinae 770
Neriocephalus Enderlein **765**
Nerioidea 758
Nesomyza Spencer *872*
Nesopsilopa Mathis & Wirth **1036**
nevadana Steyskal (Haigia) 805
niagarana (Parker) (Udamopyga) *1172*, 1173
Nicephorus Reinhard *1217*, **1248**
nidicola (Townsend) (Townsendiellomyia) 1218
niger Loew (Coniceps) *835*, 836
nigerrima (Lundbeck) (Arctopiophila) *848*
nigrans (Melander) (Sapromyza) *962*
nigriceps (Bigot) (Ursophyto) *1223*, 1257
nigriceps (Meigen) (Stearibia) *846*, 851
nigriceps Loew (Dalmannia) *752*, *753*
nigricornis (Loew) (Monochaetoscinella) *1054*
nigrinus (Zetterstedt) (Acartophthalmus) *859*, *860*, 861
nigripalpis (Malloch) (Malloewia) *1054*
nigrita (Fallén) (Delina) 1096
Nigrobonellia Brooks 1257
nigrocellulata Czerny (Cremifania) 966
nigrovittata (Malloch) (Dettopsomyia) 1012
Nilea Robineau−Desvoidy **1210**, **1211**, *1237*
Nimioglossa Reinhard **1248**
nitens (Coquillett) (Phyllophilopsis) *1216*, *1238*, *1255*
nitens (Loew) (Paramyia) 905, *907*
nitescens Frey (Chyromya) 987
nitida (Malloch) (Paraphytomyza) *873*
nitida Johnson (Heteromeringia) *855*
nitida Sturtevant & Wheeler (Diphuia) *1034*, 1038
nitidula (Coquillett) (Phorbia) *1110*
nitidula (Fallén) (Nemopoda) *947*, 949
nitidula Meigen (Diplonevra) *699*
nivalis Haliday (Leptocera) *996*, *998*
Nocticanace Malloch 1080, *1081*, **1082**
Noctiliostrebla Wenzel 1296
nomiivora Reinhard (Euphytomima) 1161
Norellisoma Wahlgren *1091*, **1093**
Nostima Coquillett 1029, **1041**
notabilis (Zetterstedt) (Pegomya) *1107*, 1108
notata (Loew) (Bertamyia) 683, *684*, *687*
notata (Wiedemann) (Euxesta) 801, *803*
notata Osten Sacken (Brachyopa) *728*
Nothybidae 898
Nothyboidea 898
notialis Reinhard (Chesippus) 1206
Notiphila Fallén 1028, 1029, *1035*, **1039**, *1040*, **1041**, *1044*
Notiphilinae 1029
Notochaetini **1174**
Notogramma Loew 801, *802*, **806**
novemmaculata Wood (Steleoneura) 1228, *1255*
Nowickia Wachtl 1244
nox Hall (Tsugaea) 1210
nudata Cresson (Canace) 1080
nudatus (Cresson) (Canaceoides) *1081*, 1082
nudiseta (Wulp) (Synthesiomyia) *1122*, 1124
nudus (Coquillett) (Oedenops) 1041
Nupedia 1106
Nupedia Karl **1108**
Nycteribia Latreille 1287
Nycteribiidae 1274, **1283**, 1297
Nycteribiinae 1289, 1297
Nycteriboscinae 1294, 1295, 1296, 1297
Nycterophilia Ferris 1294, 1297, **1298**, *1299*
Nycterophiliinae 1294, 1295, 1296, 1297, **1298**
Nycterophiliinae 1297
oarus (Walker) (Brachypalpus) *726*, 736
obesa (Fabricius) (Ornidia) *725*, 737
obesa (Loew) (Rhinoleucophenga) 1016
obesus Coquillett (Trixodes) 1249
oblata Townsend (Opsidiopsis) 1182
obliqua (Say) (Allograpta) *730*
obliqua (Say) (Tomoplagia) *823*
obliquefasciatum (Macquart) (Zodion) *752*
obscura (Coquillett) (Buquetia) 1214
obscura (Coquillett) (Macquartia) *1226*
obscura (Fallén) (Scathophaga) *1089*, *1091*
obscura (Malloch) (Spilogona) 1124
obscura (Townsend) (Angioneura) *1139*, *1141*
obscura Spencer & Stegmaier (Calycomyza) 877
obscurella (Fallén) (Discocerina) 1028, *1031*, *1037*
obscurella (Fallén) (Meoneura) *910*
obscurella (Zetterstedt) (Trichopalpus) *1089*, 1095
occidensis (Walker) (Thecophora) *752*
occidentalis (Melander & Brues) (Puliciphora) *707*
occidentalis Curran (Lonchoptera) 679
occidentalis Sturtevant (Periscelis) 897
occidentata Malloch (Phora) *689*
occidua (Fabricius) (Sarcophagula) *1165*, *1175*
occipitalis Melander (Mumetopia) *888*, *889*
ocellaris group (Leucopis) **970**
ocellaris Malloch (Leucopis) *968*
ochripes (Meigen) (Spelobia) 1003
Ochrocera Townsend **1249**
Ochthera Latreille 1028, 1029, **1030**, *1042*
oculata Fallén (Heteromyza) 973, *976*, 978
Ocyptamus Macquart 715, 716, 718, **720**
ocypterata Townsend (Aphria) *1231*
Ocytata Gistel 1198
Odinia Robineau−Desvoidy *863*, 864, **866**
Odiniidae **863**, 871
Odiniinae **866**
Odontoloxozus Enderlein *769*, *770*, **770**
Odontomera Macquart 834, *835*, **837**
Oebalia Robineau−Desvoidy 1160, *1179*, **1182**, *1183*
Oedemagena Latreille 1150, **1157**
Oedematocera 1233
Oedenops Becker **1041**
Oedicarena Loew **824**
Oedopa Loew *800*, **806**
Oedoparena Curran 924, **926**
Oestridae **1147**, 1189, 1195
Oestridae, table 1151
Oestrinae 1149, 1152
Oestrini 1148
Oestrophasia Brauer & Bergenstamm *1217*, *1242*, **1260**
Oestrus Linnaeus *1147*, 1148, 1149, 1152, *1153*, **1156**, **1157**
Oidematops Cresson *930*, **931**, **937**
Okeniella Hendel *1092*, **1094**
Okenina Malloch 1094
Olcella Enderlein 1052, *1054*, *1061*, **1064**
Oldenbergiella Czerny 974, 975, **978**
Olenochaeta Townsend 1203
Olfersia Leach *1275*, **1277**, *1278*
Olinea Richards 1004
olivaceus Townsend (Rhachoepalpus) *1246*, 1247
Omapanta Schmitz **706**
Omomyia Coquillett 833, 834, *835*, **836**
Omotoma Lioy 1206
Oncodometopus Shewell *959*, *960*, **963**
Onychogonia Brauer & Bergenstamm **1203**, *1208*
onyx Steyskal (Pseudacteon) *693*, *698*, *705*
opaca (Coquillett) (Megapariopsis) *1234*, *1241*, 1249
opaca Townsend (Hypertrophomma) *1232*
Opacifrons Duda **997**, *998*
opacum Townsend (Hypertrophomma) 1212
Opalimosina Roháček **1003**
Opelousia Townsend 1136
Opelousia Townsend 1189
Opesia Robineau−Desvoidy 1194, *1217*, **1265**
Opetia Meigen 683
Opetiinae 681, 682, **683**

Opetiophora Loew 1050, **1051**, *1056*
Ophiomyia Braschnikov 869, 871, 872, *873*, *874*, **875**
Ophirion Townsend 1198
Ophyra Robineau–Desvoidy 1118, 1127
opifera (Coquillett) (Opsophyto) 1173, *1177*
Oplogaster Rondani **1126**
Opomyza Fallén 882, *883*, **885**
Opomyzidae **881**, 890, 1009
Oppiopsis Townsend *1165*, **1178**
Opsidia Coquillett **1182**
Opsidiopsis Townsend **1182**
Opsidiotrophus Reinhard **1182**
Opsiomyia Coquillett **1095**
Opsodexia Townsend 1134, 1136, *1137*, *1139*, **1140**, *1141*, *1142*
Opsodexiinae 1135
Opsodexiopsis Townsend 1189
Opsolasia Coquillett **1124**
Opsomeigenia Townsend **1236**, *1243*, **1266**
Opsophyto Townsend **1173**, **1174**, *1177*
Opsotheresia Townsend **1248**
Oraphasmophaga Reinhard *1205*, **1213**
Orasturmia Reinhard **1206**
Orbellia Robineau–Desvoidy **978**
orbitalis (Melander) (Paraphytomyza) *876*
Orellia Robineau–Desvoidy **825**
Orestilla Reinhard **1248**
Organomyia Townsend 1210
orichalcea (Zetterstedt) (Opsolasia) 1124
orientalis (Coquillett) (Dichocera) 1198
orientalis Schiner (Atherigona) *1119*, 1125
Ormia Robineau–Desvoidy 1198, *1217*, *1234*, **1264**
ornata (Johnson) (Spilochroa) *982*
ornatipes (Johnson) (Homoneura) *961*
Ornidia Lepeletier & Serville 715, *725*, **737**
Ornithoctona Speiser *1275*, *1278*, **1277**
Ornithoica Rondani **1274**, *1275*, *1276*
Ornithomya Latreille *1271*, 1272, 1274, *1276*, **1277**, *1279*
Ornithomyia 1274
Ornithomyinae **1274**
Orthacheta Becker **1095**
Orthellia Robineau–Desvoidy 1118
Orthonevra Macquart 716, 717, 718, *726*, *728*, **732**
orthorrhaphous Brachycera 679
Orthosimyia Reinhard **1251**
Orthovena Kessel & Buegler 683
Orygma Meigen **946**, *947*
Orygmatinae **946**
Oscinella Becker 1050, *1053*, 1055, *1056*, *1059*, **1060**
Oscinellinae 1050, **1051**
Oscinidae 1072
oscinina (Fallén) (Siphonella) *1054*, 1058
Oscinisoma Lioy *1054*, **1055**, *1056*
Oscinoides Malloch 1055
ostiorum (Curtis) (Ceratinostoma) 1090
Ostracophyto Townsend *1227*, **1261**
Oswaldia Robineau–Desvoidy **1236**, *1243*, *1245*
Otites Latreille 807, **808**
Otitidae **799**, 810, 834
Otitinae 801
ovata Stein (Coenosia) *1123*
ovinus (Linnaeus) (Melophagus) 1272, 1273, 1274, *1279*, 1280
ovis Linnaeus (Oestrus) *1147*, 1152, *1153*, 1156
Oxyna Robineau–Desvoidy **828**
Oxynops Townsend **1228**
Oxysarcodexia Townsend **1163**, *1164*, *1167*
pacata Reinhard (Wagneria) *1219*
Pachycerina 954
pachycondylae (Brues) (Cataclinusa) *693*, *698*, 708
Pachyconops Camras **754**
Pachyneura Zetterstedt 866
pachyneura (Loew) (Triphleba) *699*, *700*
Pachyopella Shewell **954**, 959
Pacidianus Reinhard 1206
pacifica (Cresson) (Setacera) *1037*
pacifica (Curran) (Kirbya) *1238*
pacifica (Kessel) (Grossoseta) 683, *684*, *685*
pacifica (Melander) (Phytoliriomyza) *874*
Palaeomyopa 751
Palaeophytobia Süss & Müller-Stoll 872
Palaeosepsis Duda **949**
Palaeosicus 751
Palaeotimia Meunier 924
palliceps Johnson (Pterogramma) *996*, *997*
pallida (Fallén) (Megaphthalma) 1093
pallida (Loew) (Cadrema) 1051, *1056*, *1059*, *1061*
pallipes (Fallén) (Ocytata) 1198
pallipes (Say) (Compsobata) *762*
Palloptera Fallén 840, **842**
Pallopteridae **839**
Pallopterinae 842
Pallopterites 842
Palpada Macquart 718, **741**
palpalis (Coquillett) (Chaetosa) *1089*
palpalis (Robertson) (Robertsonomyia) *752*
palpatum (Hendel) (Piophilosoma) 845
Palpexorista Townsend 1221
Palpostomatini 1198, 1201
Palumbia Rondani 718, **741**
Pamelamyia Kessel 683
Pandasyopthalmus Stuckenberg 718, **722**, *735*
Panzeria Robineau–Desvoidy *1227*, **1261**
Paracacoxenus Hardy 1012, *1013*, *1014*, **1016**
Paracantha Coquillett *823*, **828**
Parachaeta Coquillett 1213
Paracoenia Cresson 1028, 1029, *1040*, *1042*, **1045**
Paracollinella 997
Paractora Bigot 924
Paradejeania Brauer & Bergenstamm **1244**, *1246*
Parademoticus Townsend 1264
Paradidyma Brauer & Bergenstamm *1209*, **1218**, **1253**, **1254**
Paradmontia Coquillett *1222*, **1253**
Parafischeria Townsend 1264
Paraglenanthe Wirth **1039**
Paragus Latreille 718, **722**, *735*
Paraleucopis Malloch 966, **967**, *968*, *969*
Paralimna Loew *1035*, **1041**, *1042*
Paralispidea Townsend 1224
parallela Reinhard (Torosomyia) *1205*, 1214
Parallelomma Becker **1096**
Parallelomma Becker 1090
Paralucilia Brauer & Bergenstamm *1138*, **1140**
Paramacronychiinae 1200
Paramacronychiini 1160, 1161, 1162, **1178**
Paramuscopteryx Townsend 1224
Paramycodrosophila Duda **1012**
Paramyia Williston 904, **905**, *907*
parancilla Townsend (Frontiniella) 1215
Paraneossos Wheeler 975, **978**, 982
Paranthomyza Czerny 890
Paraphasmophaga Townsend **1213**
Paraphorantha Townsend 1258
Paraphrissopoda Townsend **1168**
Paraphytomyza Enderlein *873*, *876*, **878**
Parapiophila McAlpine **852**
Paraplatypeza Kessel & Maggioncalda 683, *685*, **686**, *687*, **688**
Paraporia Townsend 1262
Paraprosalpia Villeneuve 1102, *1105*, *1107*, **1109**, *1110*, **1113**
Pararchytas Brauer & Bergenstamm **1244**
Parasarcophagini 1162, **1168**
Parasetigena Brauer & Bergenstamm **1221**, *1256*
parasocia Clausen (Parydra) *1035*, *1040*
Parasphaerocera Spuler **1004**
Parasyrphus Matsumura **720**, *733*
Paraterellia Foote **821**
Paratheresia Townsend 1248
Paratidia Malloch *1088*, **1090**

Paratissa Coquillett *1031*, **1033**
Paratraginops Hendel 864, 866
Paratrichobius Costa Lima *1293*, **1298**
Paratrixoscelis Soós 982
Parectecephala Becker *1056*, **1066**
Paregle Schnabl **1106**, 1108
Paregle Schnabl 1106
Parepalpus Coquillett *1246*, **1247**
Pareuthychaeta 1022
Parhelophilus Girschner *728*, *735*, **738**
Paroedopa Coquillett **806**
Paroxyna Hendel *824*, **829**
partita (Meigen) (Hylemyza) 1108
parva Townsend (Lixophaga) *1235*
parvicella (Coquillett) (Phytomyza) 878
parviceps (Malloch) (Thaumatomyia) 1065
parvipennis (Spuler) (Aptilotus) *1001*
parvipes Townsend (Hypertrophocera) *1223*, 1253
parvula Loew (Tethina) *1073*
Parydra Stenhammar 1029, *1035*, *1040*, **1041**
Parydrinae 1027, 1028, 1029, **1030**, **1039**
Patelloa Townsend **1206**, *1234*
paterna Dodge (Sarcofahrtiopsis) *1166*
pauxillus (Williston) (Chalcosyrphus) *725*, *733*, 734
Paykullia Robineau–Desvoidy 1188
pecchiolii Rondani (Eggisops) 1136
pecorum (Fabricius) (Gasterophilus) 1150
pecosensis (Townsend) (Phryxe) *1205*, *1234*, *1237*
pedicularidis Spencer (Phytomyza) *873*
pedunculata (Hall) (Cucullomyia) 1169
Pegohylemyia Schnabl *1103*, *1105*, 1109, *1110*, **1112**, **1113**, **1114**
Pegomya Robineau–Desvoidy 1102, **1106**, *1107*, **1108**, **1109**, **1113**, **1114**
Pelatachina Meade 1221, **1225**, *1232*, *1245*
Pelecocera Meigen *719*, **723**
Peleteria Robineau–Desvoidy *1219*, **1239**
Pelignellus Sturtevant & Wheeler 1030, *1034*, **1038**, **1039**
Pelignus Cresson 1030, **1036**, *1037*
Pelina Haliday 1028, 1029, *1037*, *1040*, **1043**
pellucida Coquillett (Pelatachina) *1232*, *1245*
Pelomyia Williston 1074, **1075**, *1076*, *1077*
Pelomyiella Hendel 1074, **1075**, *1076*, *1077*
Peltopsilopa Hendel 1028
penelope (Osten Sacken) (Procecidocharoides) *822*
Penesymmetria Kessel & Maggioncalda 683, *684*, **686**
Penetagromyza Spencer 869
Penicillidia Kolenati 1283, *1284*, 1285, 1286
penitalis (Coquillett) (Eriothrix) *1230*, *1256*, 1262
pennipes (Fabricius) (Trichopoda) *1243*
Pentacricia Stein 1118, **1125**
Penthosia Wulp *1227*, **1259**
Peratomyia Vockeroth *1088*, **1096**
peregrinum (Meigen) (Euryomma) *1122*
pergandei (Williston) (Pelecocera) *719*, 723
Pericyclocera Schmitz *692*, *698*, **704**, **706**
Periscelidae **895**, 917
Periscelidea 898
Periscelis Loew *895*, *896*, *897*, 898
Periscepsia Gistel *1226*, **1253**
perlongum Coquillett (Zodion) *753*
Peronyma Loew **825**
petiolata Borgmeier (Stenophorina) *707*, 708
petiolata Coquillett (Sphegina) *733*
petrei Mesnil (Opomyza) *883*
petrolei (Coquillett) (Helaeomyia) 1036
Phaenicia Robineau–Desvoidy *1138*, **1140**, *1142*, *1143*
Phaenopsis Townsend 1210
Phaiosterna Cresson *1035*, **1041**
Phalacrophyto Townsend **1247**
Phalacrotophora Enderlein *692*, *700*, **704**, **706**
Phalconomus Wenzel 1297
Phalcophila Wenzel 1297
Phanerochaetum Hennig 1072
Phantasiomyia Townsend **1239**
Phaonia Robineau–Desvoidy 1118, *1120*, *1123*, **1124**, **1127**, **1129**, **1130**
Phaoniinae 1116
Pharyngobolinae 1152
Pharyngobolus Brauer 1152
Pharyngomyia Schiner 1152, 1156
phaseoli (Tryon) (Ophiomyia) 871
Phasia Latreille *1217*, *1237*, *1252*, **1258**
Phasiinae 1193, 1194, 1195, 1196, 1197, 1198, 1199, 1200, 1201
Phasiini 1195
Phasiomyia Townsend 1258
Phasiops Coquillett 1198, *1223*, **1247**
Phasiostoma Townsend 1220
Phasmophaga Townsend 1198, **1225**, *1231*, **1266**
Phebellia Robineau–Desvoidy 1196, **1207**, **1212**, *1256*
Pherbecta Steyskal **934**, **937**
Pherbellia Robineau–Desvoidy 928, **929**, *930*, *933*, **937**
philadelphica (Macquart) (Homoneura) *960*, *961*
philadelphivora Spencer (Liriomyza) *876*
Philornis Meinert *1120*, **1121**, *1122*
Philotelma Becker *1037*, **1045**
Philygria Stenhammar *1035*, **1041**
Phlebosotera Duda 899, **900**, *901*
Pholeomyia Bilimek 904, *907*, **908**
Phora Latreille *689*, *690*, **701**
Phoranthella Brooks 1258
Phorbia Robineau–Desvoidy *1104*, *1107*, *1110*, **1111**, **1113**
Phoridae 679, **689**, 917
Phorinae **696**
Phormia Robineau–Desvoidy 1135, *1138*, **1140**
Phormiini 1134, 1135, **1140**
Phorocera 1206
Phorocera Robineau–Desvoidy 1196, 1197, **1221**, *1252*, *1256*
Phrosinella Robineau–Desvoidy *1183*, **1185**
Phryxe Robineau–Desvoidy *1205*, **1211**, *1234*, *1237*
Phycomyza Melander 1074
Phyllogaster Stein 1125
Phyllomya Robineau–Desvoidy *1226*, **1257**
Phyllomyini 1201
Phyllomyza Fallén 903, 904, **905**, *906*
Phyllophilopsis Townsend *1216*, **1228**, *1238*, *1255*, **1265**
phyllophora Melander (Tetanocera) *936*
Physiphora Fallén *800*, 801, *802*, **806**
Physocephala Schiner 750, **751**, *752*, *753*, **754**, *755*, **756**
Physocephalini **751**
Physoclypeus Hendel *955*, **958**
Physoconops Szilady *749*, 751, *752*, **753**
Physoptera Borgmeier *698*, **704**, **706**
Phyto Robineau–Desvoidy 1187, 1188, *1191*, **1191**, **1253**
Phytobia Lioy 870, 871, 872, **877**
Phytoliriomyza Hendel 870, 872, *874*, **877**, **878**
Phytomyptera Rondani 1195, **1220**, *1240*
Phytomyza Fallén 870, 871, 872, *873*, *875*, *876*, **878**
Phytomyzinae 869, 870, 871, **872**
picciola (Bigot) (Dioxyna) *818*
Picconia Robineau–Desvoidy *1216*, **1233**
picipes Brauer & Bergenstamm (Erythandra) *1179*
picta (Coquillett) (Amiota) 1016
picta (Fabricius) (Delphinia) *800*, *803*, 805
picta (Wulp) (Myothyriopsis) 1218, *1242*, *1243*
picticornis Townsend (Chaetoglossa) *1208*, 1213, *1234*
pictipennis (Reinhard) (Oraphasmophaga) *1205*, 1213
picturata (Snow) (Acinia) *823*, 829
Pierretia Robineau–Desvoidy **1169**, *1171*
Piezura Rondani 1118, **1121**
Pilatea Townsend 1215
pilipleura Borgmeier (Coniceromyia) *690*, *699*
pilitibia (Ringdahl) (Egle) 1111
pilosa (Staeger) (Lasiopiophila) *848*, *851*, 851
pilosifrons Allen (Phrosinella) *1183*
pinicola Malloch (Leucopis) *968*
Piophila Fallén *845*, 847, **852**
Piophilidae 842, **845**
Piophilinae 847, **851**

Piophilini 847
Piophilosoma Hendel 845, 847
piperi Knab (Microdon) *730*
pipiens (Linnaeus) (Syritta) *733*, 734
Pipiza Fallén *726*, **731**
Pipizella Rondani 729
Pipizini 715, 716, 717
Pipunculidae **745**
Pipunculinae 745, **746**
Pipunculini 745, **748**
Pipunculus Latreille *745*, 746, *747*, **748**
placata (Hutton) (Pseudoleria) 975
plagioides Townsend (Goniochaeta) *1241*
Plagiomima Brauer & Bergenstamm *1232*, **1250**
Plagiopsis Cresson 1036
Plagiosippus Reinhard 1220
planiceps (Fallén) (Gonatherus) 1095
Planinasus Cresson 891, 892
Plastophora Brues *705*, **706**
platani Süss & Müller-Stoll (Palaeophytobia) 872
platura (Meigen) (Delia) *1104*, *1110*
Platycheirus Lepeletier & Serville 718, *719*, **721**, *730*
Platycnema Zetterstedt 683
Platycoenosia Strobl 1118
Platycoenosia Strobl 1121
Platygymnopa Wirth *1031*, **1033**
Platymya Robineau-Desvoidy **1212**
platypelta (Cresson) (Calocoenia) *1037*
Platypeza Meigen *685*, **686**, *687*, **688**
Platypezidae **681**, 897
Platypezina Wahlgren 682, **683**, *684*
Platypezinae 681, **683**
Platypezininae 681, 682, **683**
Platypezoidea 679
platyptera (Loew) (Xanthomyia) *823*
Platystomatidae 801, **809**, 814
Platystyla Macquart **784**
plebeja Loew (Tetanocera) *931*, *932*
plebejus group (Hippelates) 1052
plebejus Loew (Hippelates) *1061*
Plesioclythia Kessel & Maggioncalda *681*, 683, *684*, **686**
Plethochaeta Coquillett *1089*, **1096**
pleuralis (Cresson) (Pteromicra) *930*
pleuralis Melander (Amauromyza) 877
pleuritica Loew (Cordilura) *1091*
Pleurochaetella Vockeroth 1086, *1092*, **1094**
pleuropunctata (Wiedemann) (Willistoniella) *942*
Plexiopsis Huckett 1118
plinthopyga (Wiedemann) (Kellymyia) *1166*
plumosuia (Rondani) (Kimosina) *1001*
plumosula group (Limosina) 999
Plunomia Curran **967**, *968*
pluvialis (Linnaeus) (Anthomyia) *1099*, *1107*
Pocota Lepeletier & Serville **736**
podagrica (Loew) (Morellia) *1122*
Poecilographa Melander *930*, *931*, **931**, 934
Poecilolycia Shewell *959*, *960*, **963**
Poecilominettia Hendel *956*, **958**, **964**
Poecilosomella Duda 994, *996*, *998*, **1000**
Pogonomyia Rondani 1118, 1121
Pogonomyioides Malloch 1118
Pogonortalis Hendel 809, **810**
Pogonota Zetterstedt 1086, 1087, *1088*, *1091*, *1092*, **1094**
Policheta Rondani *1217*, **1224**
Polidiini 1220
Polietes Rondani **1121**
Polietina Schnabl & Dziedzicki **1121**
polita (Coquillett) (Cordilura) *1089*, 1090
polita (Coquillett) (Aplomyopsis) 1212
polita Say (Lonchaea) *791*, *793*, *794*
polita Townsend (Epigrimyia) *1229*
polita Townsend (Gymnoprosopa) *1180*
politifrons Borgmeier (Citrago) *691*
politura (Reinhard) (Clausicella) *1229*, *1234*
politus (Say) (Toxomerus) 716
Pollenia Robineau-Desvoidy 1135, *1137*, **1140**, *1143*, 1188, 1189
Polleniini **1140**
pollinosa Walton (Eleodiphaga) *1205*
Polybiomyia Shannon *719*, **723**, *733*
Polydontomyia Williston *733*, *735*, **738**
polygrammus (Loew) (Lejops) *726*, 738
Polypathomyia Krivosheina 758, 760
polypori (Willard) (Polyporivora) *684*, *687*
Polyporivora Kessel & Maggioncalda 681, **683**, *684*, **686**, *687*
polystigma (Meigen) (Chamaemyia) *965*
Polytrichophora Cresson *1031*, **1033**
pomonella (Walsh) (Rhagoletis) *818*, *820*, *822*, *827*
ponti Vockeroth (Hydrotaea) *1123*
Porsenus Darlington 975, **977**
posticata (Fabricius) (Mallota) *714*
posticata Meigen (Nemorimyza) 877
Potamia Robineau-Desvoidy 1118, *1120*, **1127**, **1128**, *1129*
praecox Meijere (Lipoleucopis) 967, *968*
praeusta Loew (Snyderia) 1090
praeustum (Meigen) (Neottiophilum) *846*, 847, *848*
Praspedomyza Hendel *872*
pratensis (Meigen) (Blepharipa) *1243*, *1252*
pratincola (Panzer) (Anthomyiella) 1106, *1107*
pretiosa Loew (Himeroessa) 810
prima Malloch (Coenosopsia) 1102
primoris Reinhard (Orestilla) 1248
Prioriphora McAlpine & Martin 695
proboscidalis Malloch (Neohylemyia) 1108
proboscidea Zetterstedt (Cordilura) *1089*
Proboscimyia Bigot *1104*, **1108**
Procanace Hendel 1080
Procatharosia Villeneuve 1259
Procecidochares Hendel **825**
Procecidocharoides Foote *822*, **825**
Prochyliza Walker 845, *846*, **852**
Procremifania Hennig 966
Prodegeeria Brauer & Bergenstamm **1233**
Prodryomyza Hennig 924
prohibita (Aldrich) (Acanthodotheca) *1172*, *1177*
Promericia Brooks 1261
Prooppia Townsend 1201, **1207**
Prosena Lepeletier & Serville **1248**
Prosenoides Brauer & Bergenstamm *1232*, **1247**
Prospherysa Wulp **1214**, *1231*
Prosphyracephala Hennig 789
Protearomyia McAlpine *792*, 795, **796**
Protoaulacigaster Hennig 892
Protocalliphora Hough 1134, 1135, **1140**, *1143*
Protocalliphorini 1135
Protocamilla Hennig 1025
Protoclythia Kessel *684*, **686**
Protodejeania Townsend **1244**
Protodexia Townsend *1167*, *1172*, **1173**, *1176*
Protodexiini 1162, **1173**, **1174**
Protodinia Hennig 866
Protonephrocerus Collin 746
Protophormia Townsend **1140**
Protopiophila Duda *848*, **852**
Protoscinella Hennig 1050
protuberans Malloch (Macateeia) 1112
pruinosa (Macquart) (Polietina) 1121
Psaeropterella Hendel *802*, **805**
Psalidopteryx 1221
Pseudacicephala Malloch **1090**
Pseudacteon Coquillett *693*, *698*, *705*, **708**
Pseudapinops Coquillett **1263**
Pseudeuantha Townsend 1262
Pseudiastata Coquillett 1012, **1016**
Pseudocalliope Malloch *955*, **958**
Pseudoceps Becker 847
Pseudochaeta Coquillett *1208*, **1210**, **1212**

Pseudochirosia Ringdahl **1102**, *1103*
Pseudocoenosia Stein *1119*, **1126**
Pseudodinia Coquillett **967**, *968*
Pseudodoros Becker *719*, **721**
Pseudogaurax Malloch 1050, **1058**, *1059*
Pseudohecamede Hendel 1028, *1034*, **1038**
Pseudohyadina Clausen 1030, **1043**
Pseudoleria Garrett 975, **978**
Pseudoleucopis Malloch 966, **967**
Pseudolimnophora Strobl 1118
Pseudolynchia Bequaert 1274, *1276*, **1277**, *1278*
Pseudomeriana Brooks 1261
Pseudomorinia Wulp 1257
Pseudonapomyza Hendel *873*, **878**
Pseudonupedia Ringdahl *1105*, **1109**
Pseudopachychaeta Strobl *1054*, **1065**
Pseudopachystylum Mik *1252*, **1257**
Pseudoperichaeta Brauer & Bergenstamm 1210
Pseudophaonia Malloch 1121
Pseudopomyza Strobl 760
Pseudopomyzella Hennig 757, 758, 760
Pseudopomyzidae 758
Pseudopomyzinae 758, 760
Pseudopsila Johnson 784
Pseudopyrgota Malloch 842
pseudoreptans Nowakowski (Agromyza) *875*
Pseudorhicnoessa Malloch 1075
Pseudoseioptera Stackelberg **805**
Pseudosiphona Townsend 1239
Pseudostrebla Costa Lima 1297
Pseudotachinomyia Smith 1196
Pseudotephritina Malloch *802*, **807**
Pseudotephritis Johnson *804*, **807**
Psila Meigen *781*, 782, *783*, **784**
Psilacrum Becker **1055**
Psilidae 779, **781**, 788, 898
Psilinae **782**
Psilopa Fallén 1028, 1029, *1032*, **1036**
Psilopinae 1027, 1028, 1029, **1030**, **1038**, **1039**
Psilopleura Reinhard *1231*, **1251**
Psiloplogia Czerny 982
Psilosoma Zetterstedt 782, **784**
Psilota Meigen 718, *724*, **731**
Pterallastes Loew **738**
Pteremis Rondani 995, *996*, **997**, *998*
Pteridomyza Nowakowski *872*
Pterogramma Spuler 995, *996*, *997*, **1000**
Pteromicra Lioy 928, **929**, *930*, **937**
Ptilodexia Brauer & Bergenstamm *1245*, **1249**
Ptilomyia Coquillett 1027, *1034*, **1038**
Ptychoneura Brauer & Bergenstamm 1160, 1161, *1180*, **1182**
pubera (Loew) (Atrichomelina) 929, *935*, *936*, 937
puberula (Zetterstedt) (Borboropsis) 975, *976*
pudica Meigen (Cordilura) *1089*
pulchella (Williston) (Orthonevra) *726*, *728*
Puliciphora Dahl *707*, **710**, **711**
pulla (Adams) (Thaumatomyia) 1065
pulla Coquillett (Mauromyia) *1222*
Pullimosina Roháček 994, **1002**, **1003**
pullula (Zetterstedt) (Pullimosina) 994
pullus (Wiedemann) (Amphicnephes) *811*
pulverea (Coquillett) (Prospherysa) *1231*
pulvinariae Malloch (Leucopis) *969*, 970
pumilionis (Bjerkander) (Chlorops) 1050
punctata (Coquillett) (Toropamecia) *968*
punctata Fabricius (Dalmannia) *755*
Puncticorpus Duda 995
punctifrons (Becker) (Olcella) 1052
punctifrons Curran (Salpingogaster) *727*, *735*
punctigera Coquillett (Paroedopa) 806
punctipennis (Wiedemann) (Paralimna) *1042*
punctulata Williston (Nausigaster) *733*
punctum (Linnaeus) (Sepsis) *945*
punctum Meigen (Campichoeta) 1022
pusilla (Coquillett) (Opsomeigenia) *1243*
pusilla (Speiser) (Microlynchia) *1275*, 1277, *1278*
pusio group (Liohippelates) 1051
putris (Linnaeus) (Themira) *947*, *948*
Pycnoglossa Coquillett *1104*, **1108**
pygmaea (Haliday) (Atissa) *1034*
pygmaea (Meigen) (Cerodontha) *873*
pygmaeus Borgmeier (Trophodeinus) *707*
pyralidis Coquillett (Pseudochaeta) *1208*
pyrastri (Linnaeus) (Scaeva) 722, *727*
Pyrgota Wiedemann *813*, **814**, *815*
Pyrgotella Curran **814**, *815*
Pyrgotidae **813**
Pyrgotinae 814
Pyrgotini 814
Pyritis Hunter *726*, **737**
Pyrophaena Schiner *721*
quadrata (Say) (Tropidia) *725*, *733*
quadrata (Sturtevant) (Microdrosophila) *1013*, 1017
quadratus (Say) (Platycheirus) *730*
quadricornis Melander (Neophyllomyza) *907*
quadrimaculata (Panzer) (Pipiza) *726*
quadrisetosa (Malloch) (Drymeia) *1123*
quadrisetosum (Thomson) (Calliopum) *959*, *961*
quadrivittatum Malloch (Aphaniosoma) *986*
Quadrularia Huckett 1118
quatei (Wirth) (Paracoenia) *1042*, 1045
querula (Walker) (Ravinia) *1164*, *1167*, *1184*
Rachispoda Lioy **997**, *997*, *998*
radicum (Linnaeus) (Delia) *1111*
radiospinosa Hennig (Electroclusiodes) 857
Rafaelia Townsend **1178**
Rainieria Rondani *762*, *764*, **765**, *766*, **767**
ravinia Parker (Sarcofahrtia) 1181, *1184*
Ravinia Robineau–Desvoidy **1163**, *1164*, *1167*, *1170*, *1184*
Raviniina 1162
Raviniini 1162, **1163**
Raymondia Frauenfeld 1295, 1297
reclinata (Aldrich & Webber) (Carcelia) *1204*, *1243*
regalis (Reinhard) (Megaprosopus) 1254
regina (Meigen) (Phormia) *1138*, 1140
regularis Curran (Omomyia) 834
reinhardi Sabrosky & Arnaud (Atactopsis) *1205*, 1214, *1235*
Reinhardiana Arnaud 1220
relictus Wulp (Sepedon) *936*
Renocera Hendel 927, 929, *930*, **931**, *935*, **937**
reses Giglio–Tos (Scathophaga) *1088*, *1089*
Rhachoepalpus Townsend *1246*, **1247**
Rhagoletis Loew *818*, *820*, *822*, **826**, *827*
Rhagoletotrypeta Aczél **826**
Rhingia Scopoli 717, 718, *724*, **731**
Rhinia Robineau–Desvoidy 1135
Rhiniini 1133, 1136, **1140**
Rhinoestrus Brauer 1156
Rhinoleucophenga Hendel **1016**
rhinolophi Jobling (Ascodipteron) 1296
Rhinonapaea Wirth 1030, **1041**
Rhinophora Robineau–Desvoidy 1188, 1189
Rhinophoridae **1187**, 1189, 1195, 1200, 1251, 1253
Rhinopomyzella Hennig 760
Rhinotora Schiner 989, 990, 992
Rhinotoridae **989**
Rhinotorini 992
Rhinotoroides Lopes 989, 992
Rhodesiella Adams **1055**, *1057*
rhoeo (Walker) (Drino) *1208*
Rhopalopterum Duda *1056*, **1058**
Rhopalosyrphus Giglio–Tos **729**
Rhyncophoromyia Malloch *692*, **704**, **706**
Rhynencina Johnson **821**
Rhysophora Cresson *1031*, **1033**
Rhytidops Lindner *942*, **942**

ribesii (Linnaeus) (Syrphus) *730*, *739*
Richardia Robineau – Desvoidy *833*, 834, *835*, **837**
Richardiidae **833**, 842, 946
Richardiinae **834**
richardsi Vockeroth (Masoniella) 1075, *1076*, *1077*
riparia Fallén (Ephydra) *1027*
Rivellia Robineau – Desvoidy *809*, **810**, *811*
Robackina Lopes 1169
robertsonii (Townsend) (Genea) *1231*
Robertsonomyia Malloch *752*, **754**
Robineauella Enderlein *1165*, **1168**, *1171*, *1177*
robusta (Walker) (Cairnsimyia) 990, 992
robusta Brooks (Dichocera) *1227*
robusta Cresson (Rhysophora) *1031*, 1033
roederi (Williston) (Euchaetogyne) 1247
Rondania Robineau – Desvoidy 1198, *1230*, **1260**
Ropalomera Wiedemann **942**
Ropalomeridae **941**, 946
Ropolomera *941*
roralis (Linnaeus) (Melanophora) *1187*, 1189, *1191*
rosae (Fabricius) (Psila) 782, *783*
Rosellea Rohdendorf 1168
rostrata (Hendel) (Neopelomyia) *1076*
rostrata Borgmeier (Crinophleba) *690*, 696, *699*
rostratum (Melander & Brues) (Trophithauma) *692*, 704
rottensis (Statz) (Ornithomya) 1274
rotundicornis Loew (Sapromyza) *959*, *962*
rubicundus Adams (Chlorops) *1062*
rubida (Bigot) (Myopa) *752*
rubiensis Lewis (Prosphyracephala) 789
rubricosa (Meigen) (Tricogena) 1189
Rudolfia Roháček **999**, **1000**, *1001*
rufa Cresson (Automola) 834, *835*, *836*
ruficauda (Wulp) (Copecrypta) *1219*, 1239
ruficrus Williston (Microdon) *740*
rufipennis (Macquart) (Ptilodexia) *1245*
rufipes (Macquart) (Eumetopiella) *800*, 801
rufipes Meigen (Cordilura) *1088*, *1092*
rufiventris (Coquillett) (Eusenotainia) 1181
rufiventris (Meigen) (Tephrochlamys) *976*
rufiventris Townsend (Rafaelia) **1178**
rufopicta (Bigot) (Winthemia) *1204*
rufula (Curran) (Acerocnema) *1089*
ruralis (Fallén) (Voria) *1222*, *1238*
Rutiliini 1197
rutilioides (Jaennicke) (Paradejeania) 1244, *1246*
Ruttenia Rodhain 1150
sabulosa Haliday (Anthomyza) *888*
Sacatonia Sabrosky 1050, **1064**
sagittaria (Say) (Physocephala) 751
sahlbergi (Becker) (Pogonota) *1091*
salinus Cresson (Pelignus) 1036, *1037*
Salpingogaster Schiner **720**, *727*, *735*
Saltella Robineau – Desvoidy **946**, *947*, *948*
Saltellini **946**
salvum (Aldrich) (Mecynocorpus) 1168, *1170*
Sapromyia Roback 1169
Sapromyza 963
Sapromyza Fallén 953, 954, *959*, *962*, **963**
sarcinata (Loew) (Peronyma) 825
Sarcodexia Townsend **1169**, *1171*
Sarcodexiini 1161, **1169**
Sarcofahrtia Parker **1181**, *1184*
Sarcofahrtiopsis Hall *1166*, *1175*, *1176*, **1178**
Sarcophaga Meigen 953, 1162
Sarcophagidae 953, 1135, 1136, 1152, **1159**, *1184*, 1187, 1189, 1195, 1196, 1197, 1200
sarcophagina (Coquillett) (Phalacrophyto) 1247
Sarcophaginae 1159, 1160, 1161, 1162, **1163**, *1164*, *1165*, *1166*, *1167*, *1170*, *1171*, *1172*, *1175*, *1176*, *1177*, 1199
Sarcophagini 1162, **1168**
Sarcophagula Wulp *1165*, *1175*, **1178**
Sarcophagulini 1162
Sarcotachinella Townsend **1169**
Sarothromyia Brauer & Bergenstamm *1165*, **1178**
Sarothromyiini 1162, **1178**
sarraceniae (Riley) (Sarraceniomyia) 1168
Sarraceniomyia Townsend **1168**
satanica (Bigot) (Penthosia) *1227*, 1259
satisfacta (West) (Billaea) *1223*
sativae Blanchard (Liriomyza) 871
scabra (Giglio – Tos) (Potamia) *1120*
scabrum (Aldrich) (Aphanotrigonum) *1053*, *1057*
Scaeva Fabricius **722**, *727*
scalaris (Fabricius) (Fannia) 1118, *1123*
scalaris Loew (Notiphila) *1035*
Scaptodrosophila Duda **1017**
Scaptomyza Hardy 1012, **1017**
Scatella Robineau – Desvoidy **1045**
Scathophaga Meigen *1085*, 1086, 1087, *1088*, *1089*, **1090**, *1091*, *1092*, **1095**
Scathophagidae **1085**, 1100
Scathophagidae 1086
Scathophaginae 1087
Scatophila Becker 1029, *1040*, **1045**
Scelomyza Séguy 882
Schildomyia Malloch 866
Schizactia Townsend 1220
Schizochroa 892
Schizophora 750, 1152
Schizostomyia Malloch 782, 966
Schizotachina Walker 1220
schmidti (Aldrich) (Liriomyza) 871
schmitzi group (Limosina) 1000
Schoenomyza Haliday *1119*, **1125**
schreibersi (Kuhl) (Miniopterus) 758
Schroederella Enderlein 975, **979**
Schumannimyia Papp 963
Sciadoceridae 695
Sciadophora 695
Sciochthis Malloch 840, 842
Sciogriphoneura Malloch 924
Sciomyza Fallén 928, **929**, *930*, **937**
Sciomyzidae 897, 922, **927**, 966
Sciomyzinae 929
Sciomyzinae 929
Sciomyzini 927, 928, **929**, **934**
Scipopeza Enderlein 774, **776**
scirpivora Spencer (Cerodontha) *873*
scolex (Reinhard) (Hyphantrophaga) 1207
Scoliaphleps Becker *1089*, **1090**, *1091*
Scoliocentra Loew 975, **979**
Scopeuma Meigen 1090
scordala (Reinhard) (Mystacomyia) 1211, *1234*
scotlandae Cresson (Lemnaphila) *1035*, 1041
scutellata Macquart (Pallopteral) 842
Scutops Coquillett 897, 898
seamansi Shewell (Neoalticomerus) 864, 866, *867*
securicornis Fallén (Phyllomyza) *906*
Seioptera Kirby 801, **805**
selecta (Meigen) (Bessa) 1199
semilutea (Loew) (Paratissa) *1031*, 1033
semiothisae (Brooks) (Campylochaeta) *1229*
semivitta Malloch (Allognota) *1122*, 1125
senescens Scudder (Lonchaea) 795, 954
Senopterina Macquart **810**, *811*
Senotainia Macquart **1181**
Sepedomerus Steyskal 927, **934**, **938**
Sepedon Latreille *927*, 928, 929, *930*, 931, *933*, **934**, *935*, *936*, **938**
Sepsidae **945**, 1050
Sepsidimorpha Frey **950**
Sepsinae **946**
Sepsini **946**
Sepsis Fallén *945*, *949*, **950**
Sepsisoma Johnson *835*, **837**
septentrionalis Sehgal (Liriomyza) *873*

septentrionalis Townsend (Cordyligaster) 1249
Seri Kessel & Kessel **683**, *684*
seriata (Aldrich) (Chaetovoria) *1222*, 1251
seriata (Loew) (Icterica) *823*
sericata (Meigen) (Phaenicia) *1138*, *1142*, *1143*
Sericomyia Meigen 729, **738**
Sericomyiini 717
serrata (Linnaeus) (Heleomyza) *973*
serrata (Malloch) (Poecilolycia) *959*, *960*
serva (Walker) (Opsodexia) *1137*, *1139*, *1141*, *1142*
Servaisia Robineau-Desvoidy 1161, **1173**, *1176*, *1184*
Servaisiina 1162
Setacera Cresson 1029, *1037*, **1043**
setaluna McAlpine (Neopiophila) 845, *846*, *848*, *849*, 852
Setellia Robineau-Desvoidy 834
Setellida Hendel 833, 834
seticosta (Spuler) (Thoracochaeta) 994
setifacies (West) (Lypha) *1243*
setigera (Coquillett) (Hineomyia) 1261
setinervis (Coquillett) (Thelairodoria) 1224
setipalpis Sabrosky (Phlebosotera) *901*
setipes (Coquillett) (Gueriniopsis) 1221
Setisquamalonchaea Morge **796**
setosa (Coquillett) (Hoplodictya) *936*
setosa (Coquillett) (Neophyto) *1165*, *1175*
setosa (Townsend) (Kirbya) *1219*
setosa Aldrich (Johnsonia) *1175*
setosa Coquillett (Brachicoma) *1179*, *1184*
sexsetosa Duda (Meropliosepsis) 949
sheldoni (Coquillett) (Oppiopsis) *1165*, 1178
shewelli Sabrosky (Phlebosotera) *901*
shewelli Steyskal (Boreothrinax) *815*
Shewellia Hennig 866
sialia Shannon & Dobroscky (Protocalliphora) *1143*
sialia Shannon (Cheilosia) *724*
siberita (Fabricius) (Prosena) 1248
Sicus Scopoli 751
sierricola (Townsend) (Gaediopsis) *1204*
Sigaloessa Loew 899, *901*, **902**
sigilla (Reinhard) (Tolucamyia) *1165*, 1168
signata (Aldrich & Webber) (Acantholespesia) 1211
signatus (Loew) (Pseudogaurax) *1059*
signifer (Walker) (Epalpus) *1243*, *1246*
signifera (Wulp) (Oestrophasia) *1242*
sila (Reinhard) (Neosolieria) 1261
Silba Macquart 795, **796**
silvestris (Fallén) (Paraprosalpia) *1105*, *1107*
silvestris (Robineau-Desvoidy) (Parasetigena) 1221, *1256*
similis (Cresson) (Homalocephala) *800*
similis (Townsend) (Leskia) *1230*
similis (Townsend) (Plagiomima) *1232*
simplex (Fallén) (Leucostoma) *1243*, *1252*
simplex (Loew) (Allotrichoma) *1037*
simplex Aldrich (Sarothromyia) *1165*
simplex Loew (Leucopis) *970*
simplicipes (Becker) (Pleurochaetella) *1092*, 1094
singula Spencer (Liriomyza) 878
singularis (Aldrich) (Spirobolomyia) *1177*
sinipalpis (Allen) (Allenanicia) *1180*
Sinophthalmus Coquillett **1016**
sinuata (Meigen) (Sarcotachinella) 1169
sinuata (Townsend) (Microchaetina) *1241*
Siphoclytia Townsend 1264
Sipholeskia Townsend 1264
Siphona Meigen 1194, 1198, *1232*, **1236**, 1239
Siphonella Macquart *1054*, **1058**
Siphonellopsinae 1050, **1051**
Siphonini 1201
Siphophyto 1264
Siphosturmia Coquillett **1215**
Siphunculina Rondani **1052**, *1056*
Sisyropa Brauer & Bergenstamm **1212**, *1243*
sivinskii Marshall (Ceroptera) 1000, *1001*
skinneri Coquillett (Trochilodes) *1229*
slossonae Coquillett (Lipochaeta) *1034*, 1039
smaragdi (Walker) (Lamprolonchaea) *792*, 795, 796
Snyderia James **1090**
Sobarocephala Czerny *855*, **857**
solenopsidis Brues (Commoptera) *698*, *707*, 710
solicita (Harris) (Elgiva) 928, *935*, *936*
Solieria Robineau-Desvoidy **1264**
Somatia Schiner 898
Somatiosoma 987
Somula Macquart *725*, **737**
sonchi Robineau-Desvoidy (Ensina) 826
sordida (Wiedemann) (Neogriphoneura) 954, *956*, *960*, *961*
soror (Williston) (Bombyliomyia) 1202, *1245*
Spallanzania Robineau-Desvoidy **1203**, *1208*
Spanoparea Czerny 975, **979**
Spathidexia Townsend *1252*, **1265**
Spathimeigenia 1224
spatulata (Aldrich) (Stenaulacotheca) *1177*
spatulatus Marshall (Aptilotus) 999, 1003
Spaziphora Rondani **1095**
Speccafrons Sabrosky *1053*, **1058**
speciosa (Lopes) (Speciosia) 1174, *1176*
Speciosia Roback **1174**, *1176*
speiserianum Muir (Ascodipteron) 1295
Spelobia Spuler 994, *997*, **999**, 1000, *1001*, **1003**
Sphaerina Wulp **1225**
Sphaerocera Latreille *993*, *996*, *997*, *998*, *1002*, **1004**
Sphaeroceridae 917, 987, **993**
Sphaerocerinae 994, **995**
Sphaerophoria Lepeletier & Serville 715, **722**
Sphecomyia Latreille **736**
Sphecomyiella Hendel 813, **814**, *815*
Sphegina Meigen 715, *725*, *728*, **732**, *733*
sphenofrons Reinhard (Asseclamyia) *1205*, 1214
Sphenometopa Townsend *1180*, **1182**
Sphixapata Rondani *1179*, **1181**
Sphiximorpha Rondani **723**
sphondylii (Schrank) (Saltella) 946, *947*, *948*
Sphyracephala *785*, *787*, 788, 789
Spilochaetosoma Smith *1227*, **1261**
Spilochroa Williston *982*, **983**
Spilogona Schnabl 1118, *1123*, **1124**, **1125**, **1130**
Spilomyia Meigen **732**
spilota (Curtis) (Ilythea) *1034*, *1040*
spinicornis (Loew) (Hoplodictya) *935*, *936*
spinicosta (Malloch) (Cremersia) *697*, *700*, *709*
spinidens (Malloch) (Botanophila) *1105*, *1110*
spinifera (Leach) (Olfersia) *1278*
Spinilimosina Roháček **1003**
spinimanum (Fallén) (Norellisoma) *1091*, 1093
spinipennis (Haliday) (Halidayina) 996
spinipennis (Meigen) (Triarthria) 1198, *1231*, 1257
spinipes (Coquillett) (Anevrina) *693*, *697*, *699*
spinipes americana Steyskal (Sepedon) 928
Spiniphora Malloch **696**, *699*, *700*, *709*
spinosa (Coquillett) (Chaetonopsis) *1238*, 1265
spinosa Townsend (Euceromasia) *1232*
spinulosa (Malloch) (Spiniphora) *699*, *700*
Spirobolomyia Townsend **1173**, *1177*
Spoggosia Rondani 1221
spurca Aldrich (Lutomyia) *976*
spurius (Fallén) (Chalarus) *747*
squalens (Zetterstedt) (Helina) *1123*
squamosa Grünberg (Neocuterebra) 1150
stackelbergi Krivosheina (Polypathomyia) 758
Staegeria Rondani *1088*, **1095**
Stearibia Lioy *846*, **851**
Stegana Meigen 1011, 1012, *1013*, **1016**
Steganolauxania Frey *957*, **958**, *960*
stegnus (Say) (Platycheirus) *719*
stejnegeri Aldrich (Coelopa) *919*, *921*
Steleoneura Stein **1228**, *1255*

Stenaulacotheca Townsend **1173**, *1177*
Steneretma Loew 799, **801**, *802*
Stenomicra Coquillett 890, **892**, *893*
stenommatum Wood (Masistylum) 1215, *1240*
Stenomyia Loew **806**
Stenopa Loew *822*, **825**
Stenophorina Borgmeier *707*, **708**
Stenopterina Macquart 810
Stenopyrgota Malloch **814**
Stenoscinis Malloch 1050, *1054*, **1055**, *1056*
stercoraria (Linnaeus) (Scathophaga) *1085*, 1087, *1092*
stercorarius (Robineau-Desvoidy) (Meroplius) *947*, 949
sternalis (Coquillett) (Nilea) *1237*
Stevenia Robineau-Desvoidy 1188, 1189
Steveniopsis Townsend 1220
Sthenopyga Aldrich **1178**
Stichillus Enderlein *690*, *693*, **701**
stictica (Loew) (Trypetisoma) *957*
stictica Wiedemann (Ropalomera) 942
Stictomyia Bigot *802*, **805**
stigmaticalis Becker (Chlorops) 1066
Stilbometopa Coquillett *1276*, **1277**, *1278*
Stizostrebla Jobling 1297
Stomatomyia Brauer & Bergenstamm 1221
Stomorhina Rondani *1139*, **1140**
Stomosis Melander **905**
Stomoxyinae 1116, 1117
Stomoxys Geoffroy **1118**
straminea Loew (Opetiophora) 1051, *1056*
Strauzia Robineau-Desvoidy *818*, *820*, **826**
Strebla sensu Speiser 1297
Strebla Wiedemann 1297, **1298**
Strebla Wiedemann 1297
Streblidae 1274, 1289, **1293**, 1297
Streblinae 1294, 1295, 1296, 1297, **1298**
strigatus (Fallén) (Eumerus) *727*
striolata (Wiedemann) (Siphunculina) 1052, *1056*
Strongygaster Macquart 1198, 1201, *1227*, **1260**, **1265**
Strongylophthalmyiidae 774, **777**, 782
Strongylophthalmyia Heller *777*, *779*, 782
Stuckenbergiella Cogan 982
Sturmia Robineau-Desvoidy 1218
stylata (Brauer & Bergenstamm) (Periscepsia) *1226*
Stylogaster Macquart 749, 750, 751, *752*, *753*, **754**, *755*, **756**, 1198
Stylogasterinae 749, 750, 751, **754**, **756**
subalpina Ringdahl (Acrophaga) 1136
subarcuata Borgmeier (Metopina) *693*, *698*, 708
subarcuata Johnson (Temnosira) 842
submissa (Aldrich & Webber) (Meigenia) 1224, *1235*
subnudus Sturtevant & Wheeler (Pelignellus) *1034*, 1038, 1039
subopaca Loew (Ephydra) *1042*
subpellucens (Zetterstedt) (Fannia) *1119*
subpura (Johnson) (Tephritis) *824*
subvittatum (Loew) (Cetema) *1061*
Succinasteia Hennig 900
succini (Loew) (Prosphyracephala) 789
succini Hennig (Cypselosomatites) 760
succini Hennig (Electrochyliza) 782
succini Hennig (Electrophortica) 1012
succini Hennig (Protocamilla) 1025
sugens (Loew) (Imitomyia) *1229*, 1260
Suillia Robineau-Desvoidy 974, 975, *976*, **977**
Suilliinae 975
superba (Loew) (Toxoneura) *839*, *841*, 842
Svarciella Roháček 1004
sylvatica (Meigen) (Tomosvaryella) *747*
sylvosus (Williston) Gyroconops 754
Symmetricella Kessel 683, *685*, **686**
Synchysa Vockeroth **1096**
Syneura Brues *692*, *698*, 702, **704**, **708**
Synthesiomyia Brauer & Bergenstamm *1122*, **1124**
Syritta Lepeletier & Serville 717, 718, *733*, **734**
Syrphidae **713**, *746*, 750, 966, 1201
Syrphinae 715, 716, 717, **718**
Syrphini 718
Syrphus Fabricius *713*, **720**, *730*, *739*, *740*
Tabanidae 1161, 1198
Tabanus 1198
Tachina Meigen *1193*, *1231*, **1244**
Tachinidae 1135, 1152, 1162, 1187, 1188, 1189, **1193**
Tachininae 1189, 1194, 1195, 1196, 1197, 1198, 1200, 1201, 1221
Tachinini 1194, 1195, 1199
tachinomoides (Townsend) (Chetogena) *1209*
Tachinomyia Townsend **1221**
Taeniaptera Macquart *762*, *764*, **765**, *766*, **767**
Taeniapteridae 763
Taeniapterinae 761, **765**
Tanypeza Fallén *773*, *774*, **776**
Tanypezidae **773**, 779, 788
tarandi (Linnaeus) (Hypoderma) 1149, 1150, 1156, 1157
Tarassus Aldrich 1195, 1200
tarsalis (Coquillett) (Phytomyptera) *1240*
tarsalis Fabricius (Desmometopa) *904*
tarsatus (Zetterstedt) (Parasyrphus) *733*
Tarsohomoneura Hendel **954**, *961*, *963*
Taxigramma Perris 1178, **1182**, *1183*
teevani annulipes Curran (Richardia) *835*
Telomerina Rohacek *1001*, *1002*, **1003**
Telostylinae 770
Telostylinus 770
Temnosira Enderlein **842**
Temnostoma Lepeletier & Serville 716, **734**
tenax (Linnaeus) (Eristalis) *728*, *733*, *740*, 741
tenera (Wiedemann) (Genea) *1234*
tenta Hall (Chrysagria) 1163
tentatrix Loew (Euthera) *1230*, *1242*
Tenthredomyia Shannon *729*
Tenuia Malloch 758, 760
tenuicornis Cresson (Sepedon) *935*, *936*
Tephritidae 801, 810, 814, **817**
Tephritinae **821**
Tephritis Latreille *817*, *824*, **829**
Tephritoidea 814
Tephrochlamys Loew 975, *976*, **978**
Tephromyiini 1162
Teratomyzidae 898
Teretrurini 814
tergata (Coquillett) (Euaraba) *1180*, 1182
terraenovae (Robineau-Desvoidy) (Protophormia) 1140
terraenovae Macquart (Calliphora) *1133*, *1137*, *1139*
Terrilimosina Roháček **1000**
tertiaria Meunier (Palaeomyopa) 751
tertiariae Hennig (Acartophthelmites) 857, 861
tessellata (Brooks) (Linnaemya) *1227*
testacea Melander (Anticheta) 929, *935*
testaceae Soós (Sobarocephala) 857
testudinea (Loew) (Acrotaenia) *824*, 829
Tetanocera Duméril 929, *930*, *931*, *932*, **934**, *936*, **938**
Tetanocerinae 929
Tetanocerini 927, 928, **929**, **937**
Tetanops Fallén *800*, 801, *804*, 806, **808**
Tethina Haliday *1073*, 1074, **1075**, *1076*, *1077*
Tethinidae **1073**, 1080
Tethinosoma Malloch 1075
Tetramerinx Berg *1120*, **1125**
Tetreuaresta Hendel 821, **829**
Tetropismenus Loew 806, **808**
Teuchocnemis Osten Sacken *728*, **734**, *735*, **738**
texana (Aldrich & Webber) (Acantholespesia) 1211, *1255*
texana (Reinhard) (Eucelatoria) *1255*
texana (Williston) (Physocephala) *752*, *753*
texana Disney (Microselia) 696
texana Hall (Comasarcophaga) *1165*, *1170*, *1177*
texanus (Greene) (Myrmosicarius) *692*, *697*, *700*, 703, *705*
Texasa Steyskal **805**
thatuna Shannon (Psilota) *724*

Thaumatomyia Zenker 1050, *1053*, *1059*, *1061*, **1065**
thecata (Coquillett) (Leskiopsis) *1235*, 1264
theclarum (Scudder) (Aplomya) 1211
Thecophora Rondani 751, *752*, **754**, *755*
Thelaira Robineau–Desvoidy **1263**
Thelairini 1201
Thelairodoria Townsend **1224**
Thelida Robineau–Desvoidy 975
Thelylepticocnema Townsend 1160, **1174**
Thelymyia Brauer & Bergenstamm 1207
Themira Robineau–Desvoidy **946**, *947*, *948*
Theresia Robineau–Desvoidy 1248
theutis (Walker) (Cryptomeigenia) *1209*
Thinoscatella Mathis **1045**
Thiomyia Wirth 1029, *1042*, **1045**
thompsoni Herting (Lydella) *1208*
Thompsonomyia Brooks 1257
Thomsonea Rohdendorf 1169
thoracicus Loew (Pterallastes) 738
Thoracochaeta Duda 994, 995, **999**, *1002*
Thricops Rondani *1123*, **1124**
Thyreophoridae 834
Thyreophorina 845
tibialis (Coquillett) (Metopomuscopteryx) *1226*
tibialis (Curran) (Blepharomyia) *1226*
tibialis Cresson (Mosillus) *1034*
tigrina (Fabricius) (Coenosia) *1120*, *1123*
Timavia Robineau–Desvoidy 1206
tinctipennis Malloch (Circia) 1102
tiptoni Guimaraes (Basilia) 1288
Tipulidae 1198
Titanogrypa Townsend 1161, **1169**
Tolucamyia Dodge *1165*, **1168**
tomentosa Frey (Boreopiophila) 845, 852
Tomoplagia Coquillett *823*, **828**
Tomosvaryella Aczél 745, *747*, **748**
Toropamecia Cogan **967**, *968*
Torosomyia Reinhard *1205*, **1214**
torvus Osten Sacken (Syrphus) *713*
townsendi (Snow) (Polybiomyia) *719*, *733*
Townsendiellomyia Baranov **1218**
Toxomerini 717
Toxomerus Macquart 716, 717, 718, *719*, **720**, *739*
Toxonagria Shewell *1179*, **1181**, *1183*
Toxoneura Macquart *839*, *841*, **842**
Toxopodini 946
Toxotrypana Gerstacker **821**, *822*
Toxurinae 814
Tracheomyia Townsend 1152
Tracheomyiinae 1152
Trachyleucophenga Hendel **1016**
Trachyopella Duda **1000**
Trafoia Brauer & Bergenstamm *1230*, **1262**
Traginopinae **866**
Traginops Coquillett 863, 864, *865*, **866**
transita Townsend (Dexosarcophaga) 1163, *1170*
Trepidariidae 763
Triachora Townsend 1214
triangulifera (Loew) (Strongygaster) *1227*
Triarthria Stevens 1198, *1231*, **1257**
Trichobiinae 1294, 1295, 1296, 1297, **1298**
Trichobiinae 1297
Trichobius Gervais *1293*, 1295, 1296, 1297, **1298**, *1299*
Trichochlamys Czerny 975, **979**
Trichoclusia Soós 861
Trichopalpus Rondani *1089*, **1095**
trichopleura McAlpine (Protearomyia) *792*
Trichopoda Berthold 1197, *1243*, **1258**
Trichopsomyia Williston **729**
Trichopticoides Ringdahl 1118
Trichopticus Rondani 1124
Tricimba Lioy **1060**, *1061*
tricincta (Loew) (Synchysa) 1096
Tricogena Rondani 1188, 1189
tricolor Wheeler (Latheticomyia) *757*, 758, *759*
trifolii (Burgess) (Liriomyza) 871
Trigonometopus Macquart 953, *955*, **958**, *962*
Trigonomma Enderlein *1057*, **1065**
Trigonospila Pokorny *1216*, **1236**, **1266**
trilineata (Wulp) (Sphixapata) *1179*, 1181
Trilobomyza Hendel 872
Trilophyrobata Hennig **765**
triloris Reinhard (Erucophaga) *1165*, 1178
Trimerina Macquart 1029, **1036**, *1042*
Trimerinoides Cresson 1030, **1036**
Triphleba Rondani 696, *699*, *700*, **701**
tripunctata (Wulp) (Neomuscina) *1120*, *1122*
triquetra (Olivier) (Ervia) 1262
Trisapromyza Shewell *956*, **963**
triseta (Villeneuve) (Clemelis) *1208*, 1211
triseta group (Scatella) 1045
triseta Stein (Coenosia) *1123*
tristis (Loew) (Morpholeria) 979
tristis Meigen (Lonchoptera) 678
trisulcata (Adams) (Tricimba) *1061*
Tritoconicera Schmitz *699*, **702**
Tritoxa Loew 801, *802*, **805**
Trivialia Malloch *955*, **958**
trivittata (Stein) (Pegohylemyia) *1103*
trivittata Macquart (Taeniaptera) *762*, *764*
Trixodes Coquillett **1249**
Trixoscelididae 975, **981**, 992
Trixoscelidini 982
Trixoscelis Rondani *981*, *982*, **983**
Trochilodes Coquillett *1229*, **1253**
Trochiloleskia Townsend **1264**
trompe (Modeer) (Cephenemyia) *1153*, 1156
Trophithauma Schmitz *692*, **704**, **706**
Trophodeinus Borgmeier *707*, **711**
Tropicomyia Spencer 872
Tropidia Meigen 717, 718, *725*, *733*, **734**
trossulus (Reinhard) (Myatelemus) *1208*, 1214
truncatula Loew (Pelina) *1037*, *1040*
Trupanea Schrank *823*, **828**
Trypeta Meigen **826**
Trypetinae 821
Trypetisoma Malloch *957*, **963**
Trypetoptera Hendel **934**
Tryphera Meigen **1212**, *1240*
Tsugaea Hall **1210**
Tujunga Steyskal 801, **805**
Turanodinia Stackelberg 866
turbida (Curran) (Paracoenia) 1029
tuxeni Hennig (Phanerochaetum) 1072
Tylidae 763
Tylomyia Roback **1169**
Typopsilopa Cresson **1039**
Uclesia Girschner *1219*, **1250**
Udamopyga Hall *1172*, **1173**
Ulidiinae 801
Ulidiotites Steyskal 801, **806**
umbratica (Meigen) (Hebecnema) *1128*
umbrimargo (Becker) (Beckerina) *691*, *700*
umbrosa (Snow) (Penesymmetria) *684*
umbrosus (Loew) (Oncodometopus) *959*, *960*, 963
uncinata Hendel (Clasiopella) *1032*, 1036
undata Wiedemann (Pyrgota) *813*, 814, *815*
undosa (Coquillett) (Chaetostomella) *818*, 825
unicolor Aldrich (Camptops) *1166*
unilineatus (Zetterstedt) (Megaphthalmoides) 1095
uniseta Curran (Lonchoptera) *676*, 679
univitta (Walker) (Compsobata) *762*, **765**, *766*
Uramya Robineau–Desvoidy **1262**
Uramyiini 1262
Urophora Robineau–Desvoidy **821**, *822*
Urophorinae 821

Ursophyto Aldrich *1223*, **1257**
ustulata (Zetterstedt) (Strongylophthalmyia) 779
ustulata Curtis (Helcomyza) 924
ustulata Zetterstedt (Cordilura) *1089*, 1090, *1091*
utilis (Aldrich) (Wohlfahrtiopsis) 1169
vagans Loew (Diastata) *1019*, *1020*, *1021*
vaginalis Townsend (Ochrocera) 1249
valens (Aldrich & Webber) (Nilea) *1237*
Valentibulla Foote & Blanc *823*, **828**
valida (Harris) (Sphecomyiella) 814, *815*
valida (Townsend) (Microchaetina) *1234*
valida Loew (Tetanocera) *931*
vallicola Reinhard (Orasturmia) 1206
vanderwulpi (Townsend) (Chaetonodexodes) 1228, *1245*
Vanderwulpia 1229
Vanderwulpia Townsend **1260**
vandueseni (Maa) (Penicillidia) 1283
vanduzeei Cresson (Coelopa) *921*
variabilis (Coquillett) (Lixophaga) *1256*
varicolor Coquillett (Plethochaeta) *1089*
varicornis (Curran) (Brooksiella) 1094
varipes (Coquillett) (Leptopsilopa) *1032*
varipes (Meigen) (Liopiophila) *848*, 852
varipes (Walker) (Cordilura) *1091*
varipes Coquillett (Pseudodinia) *968*
varipes Loew (Myolepta) *724*, *733*
varipes Macquart (Phytomyza) 870, *875*
velutina (Loew) (Paraplatypeza) *687*
venosa Wulp (Megaparia) 1248
ventralis Aldrich (Dexia) 1248
venusta (Reinhard) (Pseudochaeta) *1208*
vernata West (Wagneria) *1234*
Verrallia Mik 746, *747*, **748**
versicolor (Loew) (Diplotoxa) *1056*, *1057*
vertebrata (Say) (Zelia) *1217*
verticalis (Reinhard) (Trigonospila) *1216*
vesicata (Huckett) (Delia) 1113
vesiculata (Borgmeier) (Physoptera) *698*
vetusta Heer (Cordilura) 1087
vexans (Curran) (Opsomeigenia) *1243*
vexatrix (Osten Sacken) (Adejeania) *1232*, 1244
Vibrissina Rondani *1209*, **1224**, **1236**
Vibrissotheresia Reinhard 1248
vicina (Walker) (Ornithoica) *1275*, *1276*
vigil (Walker) (Wohlfahrtia) *1179*
villosus Bigot (Merapioidus) *725*, 736
virginiensis (Drury) (Milesia) *728*
viridinota Brues (Phora) 701
vittata (Coquillett) (Peratomyia) *1088*, 1096
vittatum (Meigen) (Parallelomma) 1096
vittatus Loew (Trigonometopus) 962
vittigera (Coquillett) (Zonosemata) *822*
vittigera (Coquillett) (Trisapromyza) 956, 963
Viviania 1225
Volucella Geoffroy 716, 717, *728*, **737**, *740*
Volucellini 715
Volucellosia Curran 737
volucris (Wulp) (Euboettcheria) 1168
volucris Osten Sacken (Eupeodes) *735*
vomitoria (Linnaeus) (Calliphora) *1137*
Voria Robineau-Desvoidy *1222*, *1238*, **1250**
Voriini 1195, 1196, 1201, 1250
vulnerata (Loew) (Stenopa) *822*
Wagneria 1253
Wagneria Robineau-Desvoidy *1219*, *1234*, **1250**
Wagneriini 1201
washingtoniana (Bigot) (Phyllomya) *1226*
Waterhouseia Malloch 890
watsoni Hardy (Apetaenus) 1074
webberi (Smith) (Phorocera) *1252*, *1256*
wheeleri (Hough) (Paralucilia) *1138*, 1140
wheeleri (Sturtevant) (Periscelis) 897
wheeleri Brues (Apocephalus) *691*, *705*
wheeleri Brues (Ecitomyia) *707*, 710
willingii (Smith) (Lejops) *726*, 741
Willistoniella Mik **942**, *942*
willistonii (Snow) (Chamaesyrphus) *724*
Winthemia Robineau-Desvoidy *1204*, **1206**, **1210**, *1237*
Winthemiini 1195, 1196, 1197, 1201, 1210
wirthi Marshall (Pteremis) 997
Wohlfahrtia Brauer & Bergenstamm 1162, *1179*, **1181**
Wohlfahrtiopsis Townsend **1169**, *1171*
woodi Shewell (Ptychoneura) *1180*, 1182
Woodiphora Schmitz *691*, **702**
Xanionotum Brues 696, *700*, *705*, **710**, **711**
Xanthaciura Hendel **828**
Xanthacrona Wulp **807**
Xanthandrus Verrall **721**, *730*
Xanthocera Townsend 1261
Xanthoepalpus Townsend **1244**, *1246*
Xanthogramma Schiner **721**
Xanthomelanodes Townsend *1243*, **1259**
Xanthomyia Phillips *823*, **828**
Xanthophyto Townsend **1202**, **1220**, *1235*
xanthostoma Walker (Prochyliza) 845, *846*
Xenanthomyza 892
Xeniconeura Shewell *955*, *957*, **958**
Xeniomyza Hering 869
Xenochaeta Snow **828**
Xenochaetina Malloch *955*, **958**, *960*
Xenoleucopis Malloch *968*, **970**
Xenolimosina Roháček **1000**
Xenophytomyza Frey 870
Xenopterella Malloch *957*, **964**
Xylota Meigen 718, *726*, **736**
Xylotodes Shannon 734
Xylotomima Shannon **734**
yokohama Kuwana (Crytochetum) *1070*
Zacompsia Coquillett **806**
Zagonia Coquillett 981, *982*, **983**
Zara Robineau-Desvoidy 1198, **1225**
zeda Marshall (Minilimosina) 1000
Zeia Robineau-Desvoidy *1217*, **1249**
Zenillia 1206
Zenillia Robineau-Desvoidy 1207
Zentula D.K. McAlpine 992
Zeros Cresson **1039**, *1040*
Zizyphomyia Townsend **1218**
Zodion Latreille 749, 750, 751, *752*, *753*, **754**, *755*
zonalis Curran (Uclesia) *1219*
zonata (Zetterstedt) (Pegomya) *1107*
Zonosemata Benjamin *822*, **824**
zosterae (Haliday) (Thoracochaeta) *1002*
Zyziphora Peterson & Robinson *692*, **703**